SOCIAL ECOLOGY OF *OTOMYS IRRORATUS*, *RHABDOMYS PUMILIO* AND *PRAOMYS NATALENSIS*

by

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ABSTRACT

This work sets out to describe the socio-ecological niches of Otomys irroratus, Rhabdomys pumilio and Praomys natalensis in the Natal midlands. This objective necessitated a broad-based approach in which aspects of the ecological niches, and the social behaviour and social organization of the three species were investigated in field (habitat and trapping) and laboratory (experimental and observational) studies, during the period January 1976-May 1978.

To test the assumption that the commonly sympatric O. irroratus, R. pumilio and P. natalensis are primarily adapted to habitats which differ mainly in respect of water availability, an attempt was made to define their positions on a mesic/xeric continuum. The results suggest that in terms of the parameters measured (responses to water and cover availability, and to food and water deprivation), O. irroratus is more nearly mesically adapted than is R. pumilio, with P. natalensis positioned between the two extremes. However, in the case of P. natalensis it is apparently of overriding importance that this species is adapted to disturbed habitats. The mesic habitats preferred by O. irroratus are often of limited size, but resource availability within these areas is apparently high and stable. Extensive areas of suitable habitat are available to R. pumilio, but availability of resources is seasonally variable. The disturbed habitats preferred by P. natalensis arise unpredictably in nature and, depending on the rate of ecological succession, may be short-lived; hence availability of resources to this species is highly unpredictable.

Social behaviour was studied by means of dyadic encounters in the laboratory. Communication in O. irroratus, R. pumilio and P. natalensis appears to be dominated by auditory, visual and olfactory signals

respectively, although O. irroratus also has well developed visual signals in its communicatory repertoire. These differences are explained mainly in terms of patterns of diel activity and habitat preferences: R. pumilio is adapted to bright light, and its visual signals are subtle; O. irroratus is adapted to dim light, and its visual signals involve gross changes in posture, while the use of loud, low frequency vocalizations would allow conspecifics to know their precise location in relation to one another in dense vegetation; P. natalensis is nocturnal, and hence appears to emphasize olfactory (and possibly ultrasonic) communication, which would permit transfer of information in the dark. O. irroratus is overtly highly aggressive, but agonism is ritualized; ritualization of aggression has probably evolved to allow high densities of this species to exploit limited areas of prime habitat. R. pumilio is less overtly aggressive than O. irroratus, but aggression tends to be unritualized; direct aggression probably acts as a spacing mechanism, and is possible in view of the large areas of habitat available to this species. Agonism is poorly developed and ritualized in P. natalensis, permitting high sociability and group formation in this species, and maximum exploitation of locally abundant resources.

Social organization was studied in the field (trapping studies) and by means of dyadic encounters in the laboratory. The social system of O. irroratus appears to include temporal territoriality, which would permit animals to live in close spatial association (in small areas of habitat) while seldom actually meeting. Hierarchical ranking occurs in male O. irroratus and R. pumilio, with competition in both most likely being for mating opportunities. Breeding females of these two species are intrasexually territorial, in the case of O. irroratus thereby providing dispersing young with adequate space for establishment of a home-range in

prime habitat, and in R. pumilio protecting the young against conspecific female aggression until dispersal. R. pumilio tends to aggregate in mesic refuge habitats in winter, which apparently reflects the seasonality of resource availability to this species in drier environments. P. natalensis is colonial, an adaptation facilitating maximum exploitation of temporarily abundant resources in transitory disturbed habitats. In response to intense courtship by the male, female R. pumilio appear to undergo reflex ovulation; this strategy would maximize the chances of fertilization occurring during occasional meetings between males and females. Courtship intensity is low in P. natalensis, and presumably because the colonial social system of this species ensures frequent association between potential mates, females appear to ovulate spontaneously. Sexual activity was not observed in O. irroratus.

The life-history tactics of the three species are such that O. irroratus and P. natalensis respectively appear to be K- and r-selected, with R. pumilio falling between these two extremes on an r-K continuum.

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1. INTRODUCTION

1.1. Approach to the study

This work sets out to describe how the social behaviour and social organization of three species of African rodents, the vlei rat Otomys irroratus (Brants, 1827), the four-striped mouse Rhabdomys pumilio (Sparrman, 1784) and the multimammate mouse Praomys (Mastomys) natalensis (A. Smith, 1847), are adapted to the habitats in which they most usually occur.

The study was conceived in 1976 during discussions with A.K. Lee, J. Meester and G.C. Hickman on the topic of sociobiology, as defined by Wilson (1975). It was apparent that while much basic ecological and general biological information was available on O. irroratus, R. pumilio and P. natalensis (section 1.2.1) little was known of the structure and adaptive significance of their social systems. A research project was designed, therefore, to provide information on the social behaviour and social organization of the three species, which was to be interpreted in terms of ecological parameters, availability of resources in particular. Achievement of these objectives necessitated an approach in which complementary captive studies (analysis of social organization and experimental work) and field studies (habitat and trapping) were undertaken.

The study was primarily concerned with social phenomena, but sufficient trapping was carried out to allow comparison with available ecological information on the three species (section 1.2.1), and to provide a basis for interpretation of social trends observed in captivity (Eisenberg 1967).

Trapping methods are widely used in the study of social organization (e.g. Burt 1943; Calhoun & Casby 1958; Southwood 1966; Delany 1974; Flowerdew 1976). Field observation may be useful in understanding the modes of dispersion of larger rodents (e.g. Taylor 1966; Barash 1974; Armitage 1977; Viljoen 1977), and while observational studies of free-living small rodents have been reported (e.g. Southern 1955; Kikkawa 1964; Happold 1973, 1976; Nel & Rautenbach 1974), density of vegetative cover (section 2.4.1) made this impossible in the present study. Consequently, the observational studies reported here were on captive animals, based on the techniques of Eisenberg (1967) and Happold (1973, 1976). Although Macfadyen (1975) has called for emphasis of field experimentation (e.g. Bendell 1959; Krebs & De Long 1965; Fordham 1971; Flowerdew 1972; Bradford 1975; Christian 1979a), I found it necessary to use laboratory methods in simplified environments to supplement ecological information obtained in the field (section 3).

1.2. General biology of *O. irroratus*, *R. pumilio* and *P. natalensis*

1.2.1. Synopsis of earlier studies

Until about 1970, information on *O. irroratus*, *R. pumilio* and *P. natalensis* in Southern Africa was largely restricted to taxonomy, distribution and disease transmission. Little was known of the ecology and social systems of the three species. A major exception concerned *P. natalensis*, with publications dealing with aspects of behaviour, including social behaviour in captivity (Veenstra 1958), post-natal development (Meester 1960), and reproductive ecology of a free-living population on the Transvaal highveld (Coetzee 1965, 1967). Meester & Hallett (1970) discussed post-natal development in a number of rodent

species, including the three under consideration here.

In the late 1960's and early 1970's several important studies were initiated by J. Meester and J.A.J. Nel of the Mammal Research Institute, University of Pretoria, which resulted in dissertations dealing with aspects of the biology of one or more of the three species. These studies involved largely Transvaal highveld populations, communities or stock (captive studies), and were as follows: ecology, behaviour, post-natal development and other aspects of the biology of O. irroratus (Davis 1973) and R. pumilio (Brooks 1974); social organization of confined R. pumilio (Marais 1974) and P. natalensis (Cilliers 1972); ecology of communities which included R. pumilio and P. natalensis (De Wit 1972), and P. natalensis (Swanepoel 1972). Of these studies the only one which did not take place in the Transvaal was that of Swanepoel (1972), which he undertook in Northern Natal (Zululand). To my knowledge, only three publications have resulted from these studies, on the behaviour (Davis 1972) and reproduction and post-natal development (Davis & Meester 1981) of O. irroratus, and a published version of Swanepoel's (1972) dissertation (Swanepoel 1976).

A number of studies on one or more of the three species have been undertaken in recent years. There have been two major studies on R. pumilio in the S.W. Cape, a wide-ranging ecological investigation (David 1980), and an analysis of the social organization of captive and free-living populations (Johnson 1980). C.N.V. Lloyd has completed a major ecological study of R. pumilio in the Natal midlands, but the work has not yet been published. Studies on P. natalensis include a general biological review (Coetzee 1975) and a detailed study of post-natal development of Natal midlands stock (Baker & Meester 1977). The ecological role of P. natalensis, particularly in relation to fire, was

the subject of a note in which O. irroratus and R. pumilio were also briefly dealt with (Meester et al 1979). There have been studies on the effects of fire on all three species in the Natal Drakensberg (Mentis & Rowe-Rowe 1979), and on small mammal communities in S.W. Cape montane fynbos which included O. irroratus and R. pumilio (Willan & Bigalke In press; Appendix 1), while Bigalke & Willan (In press; Appendix 2) referred to all three species in their review of the effects of fire regime on faunal composition and dynamics in South African ecosystems. A series of papers on O. irroratus and R. pumilio in the Fish River Valley, Eastern Cape, have dealt with aging criteria and population age structure (Perrin 1979), food preferences (Curtis & Perrin 1979), feeding habits (Perrin 1980a), breeding strategies (Perrin 1980b), ecological strategies (Perrin 1980c) and body fat content (Perrin 1981a); investigations of digestive tract morphology and activity patterns of a number of species of small mammals, including O. irroratus, R. pumilio and P. natalensis, were undertaken by Perrin & Curtis (1980) and Perrin (1981b), respectively. Further studies dealing with one or more of the three species include work on nest-building behaviour (Stiemie & Nel 1973), climbing behaviour (Earl & Nel 1976), distribution (Avery 1977), nest-building and activity patterns (Packer 1980), distribution along altitudinal gradients (Bond et al 1980), and heat production (Haim & Fourie 1980a, b).

Elsewhere in Africa a large number of studies have been reported which deal with various aspects of the biology of one or more of the three species. These include the following: Namibia (South West Africa): Christian (1977a, b, 1978, 1979a, b, 1980); Botswana: Smithers (1971); Zimbabwe: Choate (1971, 1972), Gordon (1978), Green et al (1978), Swanepoel (1980, 1981); Zambia: Vesey-Fitzgerald (1966), Sheppe (1972), Chidumayo (1980); East Africa: Delany (1964a, b, 1969, 1971, 1972), Dieterlen (1968), Delany & Neal (1966, 1969), Neal (1970), Hubbard (1972),

Kingdon (1974), Taylor & Green (1976), Delany & Roberts (1978), Cheeseman & Delany (1979); West Africa: Bellier (1975); and a taxonomic review for the whole continent (Misonne 1968).

It is of interest that R. pumilio colonies are maintained in the U.S.A. where a variety of captive studies have been carried out on this species (e.g. general behaviour - Dewsbury & Dawson 1979; activity patterns - Dewsbury 1980; climbing ability - Dewsbury et al 1980; post-natal development of thermoregulation - Couture 1980).

1.2.2. Taxonomy

The genus Otomys is generally regarded as belonging to the Otomyinae, a small subfamily of specialized cricetids (Dieterlen 1968; Misonne 1968; De Graaff 1981), and Kingdon (1974) speculates that this taxon shares a common ancestry with the microtines. On the basis of morphological (Misonne 1969, in Perrin 1980b) and palaeontological evidence (Pocock 1976) it appears that Otomys may represent a line of murine radiation allied to Rhabdomys (Perrin 1980a, b). However, the lamellate molars and enlarged M^3 in Otomys are not typical of murine rodents, and the genus is probably cricetid (Misonne 1969, in De Graaff 1981) rather than murid (Perrin 1980a, b). Perrin & Curtis (1980) included O. irroratus under the Cricetidae. In addition to the question of the taxon to which O. irroratus belongs (which clearly cannot be resolved without further investigation; J. Meester Pers. comm.) there are two difficulties regarding the taxonomy of this species. The first relates to the distinction, if any, between O. irroratus in Southern Africa and O. tropicalis in central Africa. A number of East African reports have referred to irroratus (e.g. Delany & Neal 1966; Dieterlen 1968; Delany 1972), and while irroratus and tropicalis may be synonymous (Davis 1972;

Misonne 1968), Davis (1973) treated them as distinct for the purpose of comparison with his own work in the Transvaal. I follow Davis (1973) in this respect, the decision resting on the confused state of Otomys taxonomy. A related problem involves the difficulty of distinguishing between species of Otomys in the field. Although it may be possible to separate irroratus and angoniensis on external characters (Davis 1973), other authors were unable to distinguish between living specimens in an irroratus/laminatus/saundersae complex (Bond et al 1980; Willan & Bigalke In press). It therefore seems that unless an extensive voucher series was identified using acceptable criteria (Misonne 1968), studies purporting to have dealt with O. irroratus (or any other species of Otomys) may be of doubtful validity. In the present study J. Meester (Pers. comm.) identified all specimens from the study areas as O. irroratus.

R. pumilio is a member of the subfamily Murinae, and is the only species of the genus (Misonne 1968).

Praomys is a diverse murine genus which parallels Rattus in being morphologically conservative and highly successful, but with close affinities to other African murids (Misonne 1969, in Kingdon 1974) rather than to Rattus (Lee & Martin 1980). There are four sub-genera and 20 species of Praomys, of which P. natalensis and four other species belong to the subgenus P. (Mastomys) (Misonne 1968). Praomys has radiated extensively in tropical Africa, but in Southern Africa only two other species of this genus are present, namely P. (Myomyscus) verreauxi and P. (Mastomys) shortridgei (Misonne 1968). P. (M) natalensis is by far the most common and widespread of these species, however (De Graaff 1981). The taxonomic status of P. (M) natalensis, hereafter referred to simply as P. natalensis, is complicated by the fact that three different chromosome forms (2N = 32; 2N = 36; 2N = 38) are known to occur within this taxon (Matthey 1966), which may therefore represent not one but

three species. These forms are apparently evolutionarily divergent since the 32- and 36-chromosome forms co-existing in Zimbabwe (Norton area) do not hybridize (Gordon 1978) and show no chromosome or haemoglobin admixture (Green et al 1978). In the Ivory Coast 32- and 38-chromosome forms are present, but occupy slightly different habitats (Bellier 1975). Hallett (1979) found the 32-chromosome form to occur in the Northern and Eastern Transvaal, Natal, Zimbabwe and Namibia (S.W. Africa), and the 36-chromosome form in the Eastern and Northern Cape, Northern Orange Free State, Southern Transvaal and Lesotho. Specimens from my study areas in the Natal midlands were karyotyped as the 32-chromosome form (J.M. Hallett Pers. comm.). No ecological or behavioural differences between these sibling species have been noted in the literature, but in view of the likelihood that such differences exist (and although they may be small) comparison of information obtained during the present study with that already existing on P. natalensis (section 1.2.1) must be tentative.

1.2.3. Morphology

O. irroratus is characterized by large, yellow, deeply-grooved incisors, as are all Otomys. It is of moderate to large size, compact and stockily built, with short legs, a blunt face, shaggy pelage and large, rounded, well haired ears. The tail is short (approximately 60% of the head-body length) and fairly well haired. The dorsal body colour is speckled buffy-brown, with the sides and ventral parts paler, the sides of the muzzle buffy to rust-coloured and the cheeks and throat paler, the tail dark brown above and buffy below, and the feet greyish (after Roberts 1951 and De Graaff 1981).

Standard measurements (mm) given by Roberts (1951) for O. irroratus are as follows:

	Head-body	Tail	Hind foot (s.u.)	Ear	Greatest skull length
Males:	140-216	90-130	28-33	20-29	38-46
Females:	147-188	82-125	24-33	18-26	37-43

These measurements indicate the occurrence of sexual dimorphism in this species, with males larger than females. This is borne out by the mass of animals trapped during the present study in Natal, and in later studies in the S.W. Cape (Willan & Bigalke In press). In both areas males occasionally weighed over 200g while females never did so, and non-parous females generally weighed less than 150g.

Morphological characters investigated by Davis (1973) included phallus/baculum structure, which was found to be of the complex type (Hooper & Musser 1964, in Davis 1973), and the structure of the digestive tract, from which it was concluded that O. irroratus has high digestive efficiency. Perrin & Curtis (1980) later showed the digestive tract of this species to be specialized for an herbivorous diet. The dentition is similarly adapted (Roberts 1951; Perrin & Curtis 1980).

R. pumilio is of medium size with a short, slightly harsh pelage, and is characterized by four blackish stripes, separated by more or less white stripes, running from the back of the head along the length of the dorsum. The tail is a little shorter (80-90%) than the head-body length, scaly, and short-haired. The ground colour is yellowish grey-brown to speckled buffy, with the chin, throat and belly whitish, the front of the face and the cheeks darker than the flanks, the ears rusty-reddish, fringed with black on the outer anterior edge, the tail dark brown above and buffy below, and the feet dull buffy. Colouration of individuals is variable, some being more yellow than the majority (after Roberts 1951 and De Graaff 1981). In addition, there are conspicuous bands of yellow hairs above and below the eyes.

Male and female R. pumilio are of similar mass (Roberts 1951; De Graaff 1981), although both in Natal and the S.W. Cape males frequently weigh over 60g, while females rarely do so (Pers. obs.). Standard measurements in mm (males and females combined; Roberts 1951) are as follows: Head-body 90-130; tail 78-135; hind foot (s.u.) 18-27; ear 10-17; greatest skull length 25-32. Regional variation in tail length relative to head-body length occurs in R. pumilio, with the western semi-desert form relatively long-tailed and the eastern form relatively short tailed (Davis 1962; Coetzee 1970), while in climatically intermediate areas tail length is also intermediate (Coetzee 1970).

R. pumilio has no specialized morphological adaptations to diet; gastric morphology is highly variable, and individual specimens may or may not possess a gall bladder and/or caecal haustra (Perrin & Curtis 1980).

The appearance of P. natalensis, which is distinguished by its having 10-12 pairs of mammae (De Graaff 1981), is typically murine, and has been described as intermediate between that of Rattus rattus and Mus musculus (Veenstra 1958). P. natalensis is medium sized, with moderately long, soft fur, ovate ears, and the sparsely haired tail about the same (seldom longer) as the head-body length. The dorsal pelage is yellowish- or reddish-brown or buffy, with the underparts varying from white to darkish grey, the tail brown above and whitish below, and the feet white with a reddish tinge (after Roberts 1951 and De Graaff 1981). Roberts (1951) draws attention to the great variation in colouration between different populations, with low cover density resulting in a paler form, and high cover density in a darker one, but there may also be considerable variation within a single population (De Graaff 1981).

In general, male P. natalensis appear to become slightly larger than females (Roberts 1951; Chapman et al 1959; De Wit 1972; De Graaff 1981); the mass of P. natalensis males and females trapped during the present study were marginally disparate, with males occasionally attaining almost 70g, but females rarely attaining 65g. Veenstra (1958) states that this species seldom exceeds a mass of 100g, and in the present study even animals which had been held in captivity for over a year rarely reached a mass of 80g. Standard measurements in mm for P. natalensis are as follows: Head-body 96-140; tail 76-129; hind foot (s.u.) 18-25; ear 15-20; greatest skull length 26-32.5 (Roberts 1951).

Although P. natalensis has no gall bladder, its dentition is typical of an omnivorous murid and it has retained a number of primitive features in the digestive tract (Perrin & Curtis 1980).

1.2.4. Geographic distribution

O. irroratus occurs widely in southern savanna highveld and in coastal, montane and sub-montane grasslands, as well as in Cape Macchia (Davis 1974) (Figure 1). It extends from the S.W. Cape through Natal, Lesotho and the Orange Free State to the Transvaal, with an isolated population on the eastern escarpment of Zimbabwe extending into Mozambique. It is largely absent from the S.W. Arid, although isolated populations exist in "oases" in this biotic zone (Davis 1962). The occurrence of these populations suggest that its range was once far more extensive than at present (Dorst 1965).

R. pumilio is generally distributed throughout Southern Africa (Figure 2) except in the eastern tropical savanna woodlands where it gives

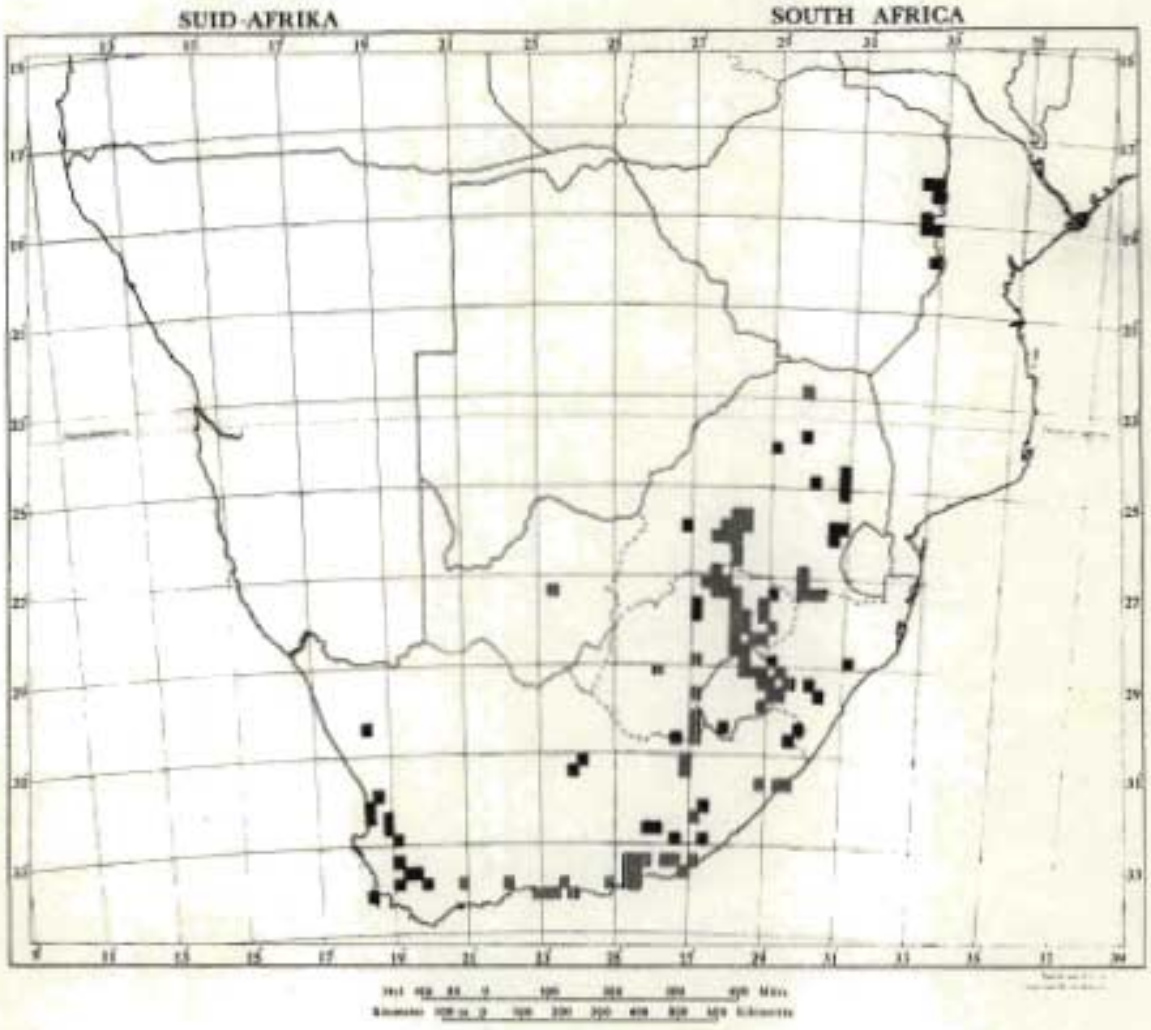

Figure 1. Geographic distribution of O. irroratus in Southern Africa (quarter-degree squares; after Davis 1974).

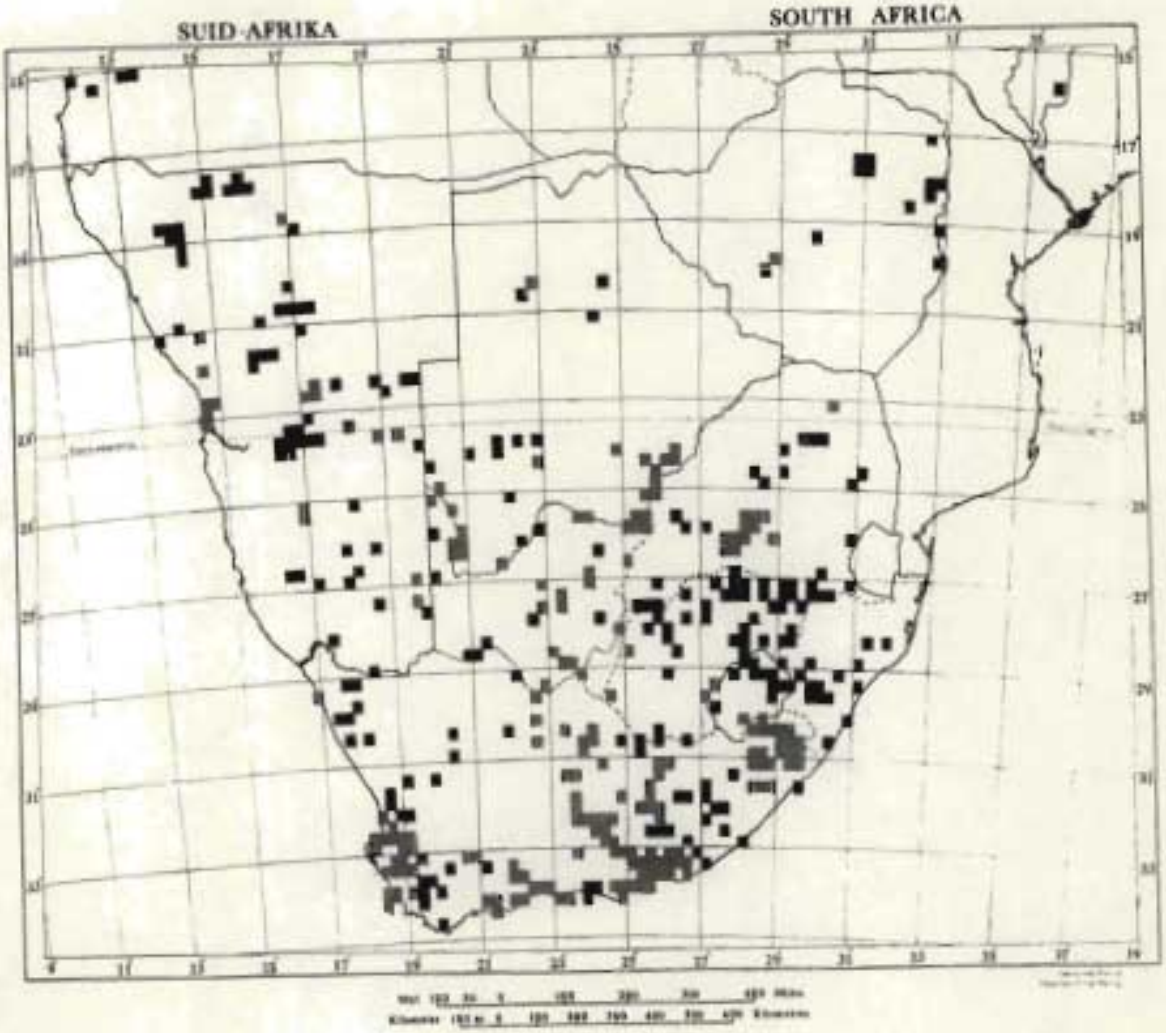

Figure 2. Geographic distribution of R. pumilio in Southern Africa (quarter-degree squares; after Davis 1974).

way to the closely related Lemniscomys griselda (Davis 1962). It extends to central Angola, southern Malawi, Tanzania, Kenya, Uganda and Zaire (Davis 1962; Misonne 1968). In tropical Africa it is restricted to montane and sub-montane grasslands from about 1700m to 3500m (Kingdon 1974), but in Southern Africa it occurs at a wide range of altitudes, from coastal grasslands and Macchia (S.W. Cape) to sub-montane habitats in the Natal Drakensberg (Mentis & Rowe-Rowe 1979). R. pumilio is primarily a savanna species but ranges extensively in the S.W. Cape and S.W. Arid Zones (Davis 1962, 1974). It has been observed in montane forest in the Natal midlands (T. Oatley Pers. comm.), but there are no published accounts supporting this observation and penetration of forest is probably localized and sporadic.

P. natalensis is widely distributed in Africa south of the Sahara, and occurs in Morocco in the Palaearctic region (Figure 3). It is widespread in both northern and southern Savanna, equally in woodlands and grasslands, but does not generally penetrate arid regions, the lowland forests of tropical Africa or the S.W. Cape (Davis 1962, 1974). It is semi-commensal, and its present distribution may be the result of its having followed early human population movements (Davis 1962; Kingdon 1974). This theory is supported by Avery (1977) who has shown that P. natalensis only colonized the Cango Valley, Southern Cape, with the arrival of White settlers in the area about 200 years ago. The southern limit of P. natalensis distribution is now thought to be along a line between Oudtshoorn and Plettenberg Bay, west of which P. verreauxi represents the genus. P. natalensis probably arose in the southern savanna but extended its range by adapting to habitats degraded by man (Kingdon 1974). Meester et al (1979) anticipate that it will become increasingly abundant with increasing human influence on the environment. However, it generally

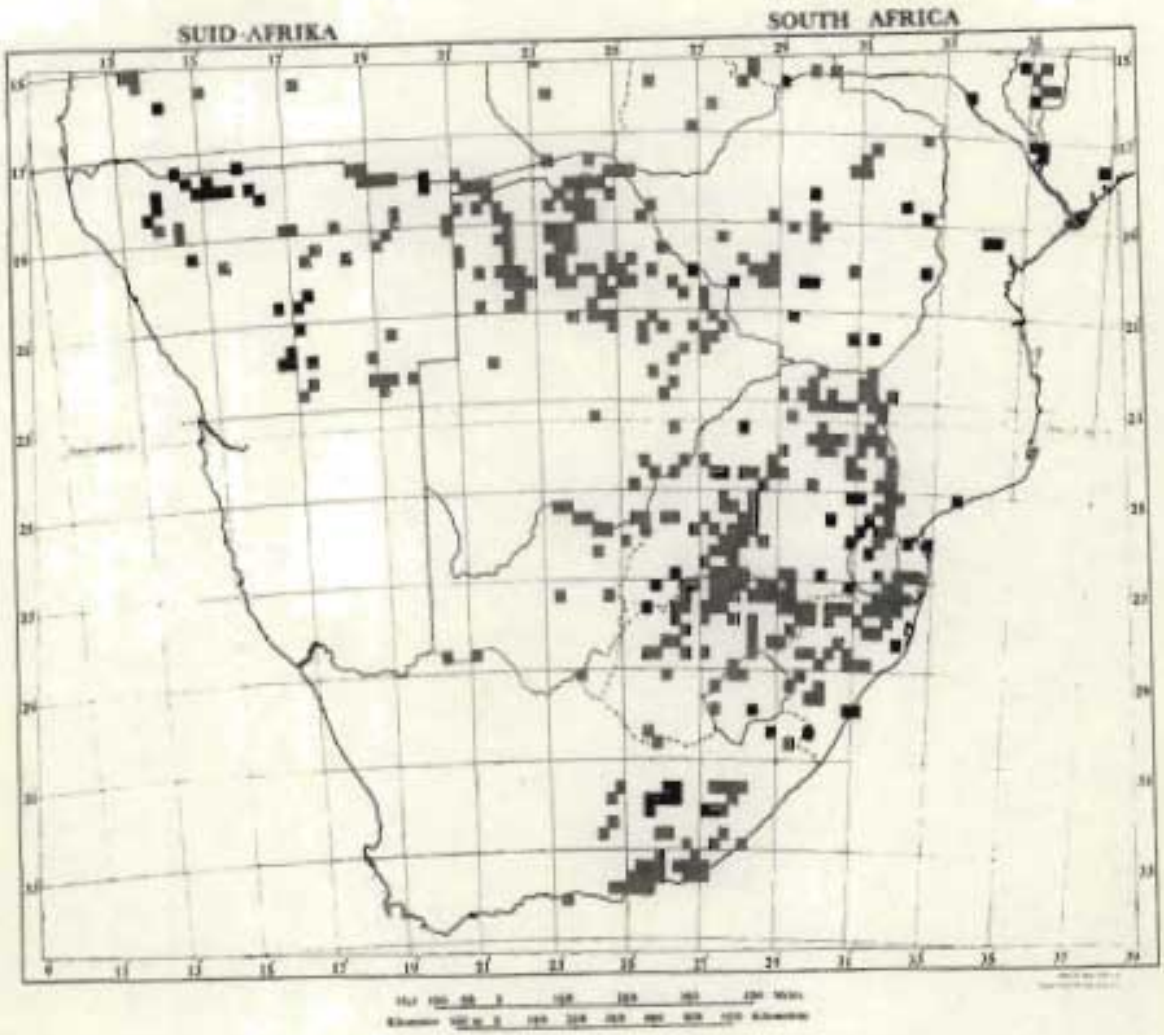

Figure 3. Geographic distribution of P. natalensis in Southern Africa (quarter-degree squares; after Davis 1974).

does not occur in large towns (Shortridge 1934), probably because it gives way to Rattus (Veenstra 1958), and it is declining in parts of East Africa where the range of Rattus rattus is expanding (Kingdon 1974).

1.2.5. Ecological distribution

The ecological niches of O. irroratus, R. pumilio and P. natalensis appear to overlap extensively, and the three species are sympatric in many parts of Southern Africa (e.g. Davis 1962, 1974; De Graaff 1981). This may be explained in terms of relative niche breadth (Miller 1967). R. pumilio occupies a broad niche within which is included that of the more specialized O. irroratus (Brooks 1974), especially in respect of feeding habits (Perrin 1980a). Meester et al (1979) have postulated that P. natalensis has even more generalized ecological requirements than R. pumilio, but this assumption needs to be carefully tested before final conclusions can be reached.

O. irroratus is regarded as preferring mesic habitats which support lush vegetation, often with wet soil and shallow standing water as found in river valleys and marshes (Shortridge 1934; Davis 1973; De Graaff 1981), but it is not restricted to such areas, and in montane grasslands may inhabit steep hillsides some distance from water (Davis 1973; Mentis & Rowe-Rowe 1979). It occurs extensively in S.W. Cape montane fynbos, often a kilometer or more from the nearest water, in areas which in summer are extremely hot and dry (Willan & Bigalke In press), and in the Eastern Cape in areas of unpredictable rainfall (e.g. Perrin 1980a).

R. pumilio occurs in a wide variety of habitats, ranging from wet and lush to entirely waterless (Shortridge 1934; Brooks 1974; De Graaff

1981). This range includes marshes, river valleys, forest margins, bush, scrub, grasslands, fynbos and dry river beds (Shortridge 1934; Hechter-Schulz 1962; Choate 1971; Smithers 1971; Brooks 1974; Bigalke 1978). In the S.W. Arid its distribution is generally limited by availability of suitable vegetation, as in dry river beds (Coetzee 1970), but it also occurs in poorly vegetated dune country in the Namib desert (P. Laycock Pers. comm.). In Malawi R. pumilio favours damp habitats supporting dense stands of bracken (Hanney 1965) or bracken-sedge-kikuyu grass (Stewart 1972), and in East Africa (Tanzania) its preference is for dense vegetation in high altitude river valleys and forest margins (Vesey-Fitzgerald 1966).

P. natalensis has wide habitat tolerances (Meester et al 1979), occurring throughout grassland and woodland savanna and in clearings in West African forests (Coetzee 1975). It is, however, absent from Cape Macchia in which both O. irroratus and R. pumilio range extensively, and does not occur in areas as dry as those penetrated by R. pumilio, for example the Namib desert (Coetzee 1975). In Southern Africa P. natalensis prefers dense bush (Veenstra 1958) or pioneer vegetation (De Wit 1972; Meester et al 1979), while in Tanzania it is found in a variety of habitats including forests, rank vegetation associated with water courses, grassland and rocky habitats (Vesey-Fitzgerald 1966). As a semi-commensal it is common around human habitation and in cultivated or otherwise disturbed areas (Veenstra 1958; Coetzee 1975; Meester et al 1979), and population densities are normally higher in such habitats than in ones which are undisturbed (Coetzee 1975).

1.2.6. Niche separation

While the niches of the three species overlap in many respects, the

fact that they are often sympatric (section 1.2.5) indicates that there must exist mechanisms whereby competitive exclusion is avoided. In this respect, differences in their requirements for food and shelter, in patterns of diel activity and in habitat utilization are probably most important.

O. irroratus is a specialist herbivore (Davis 1973; Perrin 1980a; Perrin & Curtis 1980), and competition for food with the omnivorous R. pumilio (Brooks 1974; Perrin 1980a; Perrin & Curtis 1980) and P. natalensis (Veenstra 1958; Kingdon 1974; Coetzee 1975; Perrin & Curtis 1980) is probably slight. R. pumilio and P. natalensis would be expected to compete for at least some food items, but whereas R. pumilio is mainly diurnal (Smithers 1971; Choate 1972; Brooks 1974; Christian 1977a; Dewsbury 1980; Perrin 1981b) P. natalensis is largely nocturnal (Smithers 1971; Choate 1972; De Wit 1972; Coetzee 1975; Perrin 1981b), thus probably reducing competition for food between these species. O. irroratus exhibited regular short-term activity in a captive study (Perrin 1981b), but was mainly crepuscular (with some activity throughout day and night) in Davis' (1973) field study.

P. natalensis typically occupies an underground burrow (Roberts 1951; Veenstra 1958; Choate 1972; De Wit 1972; Coetzee 1975; De Graaff 1981), while both O. irroratus and R. pumilio generally nest on the surface, at least in areas where dense vegetation exists (Roberts 1951; Davis 1973; Brooks 1974; De Graaff 1981). Information given by De Graaff (1981) suggests that R. pumilio is more inclined to burrow than is O. irroratus, but in a captive study using animals from the Natal midlands the reverse was true, although neither of these species burrowed as extensively as P. natalensis (Willan Unpubl.). In general, there may be no competition

for nest-sites between P. natalensis and the other two species, which may, however, compete for nest-sites between themselves.

Free-living P. natalensis may utilize the vertical component of the habitat (Earl & Nel 1976), but the other two species generally do not (De Graaff 1981), except that in the S.W. Arid R. pumilio is known to climb low trees and may occupy birds' nests (Shortridge 1934). The climbing ability of P. natalensis is presumably an adaptation to arboreal feeding, which may be seen as further reducing competition for food between this species and R. pumilio.

1.2.7. Social organization

O. irroratus was described by Shortridge (1934, p.240) as "not truly gregarious", although concentrated in suitable habitats. The species is now regarded as asocial and tending to adult isolation (Davis 1972, 1973), as is the possibly synonymous O. tropicalis (Dieterlen 1968; Kingdon 1974).

R. pumilio was originally thought to be communal (Powell 1925), but this was contradicted by Shortridge (1934) and Choate (1972), the latter suggesting that males are intolerant of one another and occupy well separated areas. However, R. pumilio is now thought to be dispersed according to a complex hierarchical/territorial system (Brooks 1974; Marais 1974; Johnson 1980), but with a tendency to aggregation during the period of winter reproductive quiescence (Brooks 1974). In the Kalahari R. pumilio tends to be more sociable than in wetter areas, and apparently forms cohesive social groups (Nel 1975).

Shortridge (1934, p.301) regarded P. natalensis as "not truly gregarious", but subsequent authors have described the species as highly

sociable (Ansell 1960; Coetzee 1967, 1975; Choate 1972; Kingdon 1974), and territoriality is thought to be poorly developed (Veenstra 1958; Cilliers 1972; De Wit 1972). Social cohesion appears to be maintained by means of hierarchical ranking (Cilliers 1972).

1.2.8. Relationships with man

All three species have been implicated in the transmission of diseases infecting man, and many accounts exist of economic loss resulting from their activities. These aspects have been the subject of reviews comprehensively dealing with O. irroratus (Davis 1973), R. pumilio (Brooks 1974) and P. natalensis (Cilliers 1972; De Wit 1972). Consequently, only the most important features are discussed here.

P. natalensis is one of the principle African carriers of zoonotic diseases such as plague (Davis 1964) and Lassa Fever (Coetzee 1975), and on account of its semi-commensal habit readily transmits such diseases to man (Davis 1964; Coetzee 1965, 1975). In East Africa Rattus rattus may be more important in transmitting plague to humans, becoming itself infected through contact with P. natalensis (Kingdon 1974). The plague bacillus has also been isolated from O. irroratus and R. pumilio, but although these species may serve as wild reservoirs along with the primary host Tatera brantsi, they relatively infrequently come into contact with man and thus are probably less important vectors than is P. natalensis. R. pumilio is a carrier of a number of haemorrhagic viruses which may be lethal in man (J.W. Moodie Pers. comm.). Other pathogens have been isolated from one or more of the three species, but they do not have the same serious implications as those referred to above.

Both R. pumilio and P. natalensis have been cited as causing damage to cereal crops (De Wit 1972; Delany 1972), and P. natalensis may consume a variety of stored grains and other products (Vesey-Fitzgerald 1966; Kingdon 1974). O. irroratus appears not to be implicated in this type of damage (Shortridge 1934), but together with R. pumilio is responsible for extensive loss in timber growing areas, where young exotic trees, mainly conifers, are destroyed by ring-barking as the cambial layer is eaten (Davis 1942; Hechter-Schulz 1962; Davis 1973; Hopf et al 1976). Several papers have dealt with the problem of rodent damage in exotic plantations in Southern Africa (Davis 1942, 1966; Hechter-Schulz 1951, 1962; MacKellar 1952).

2. METHODS

2.1. Introduction

A number of techniques were employed in both the field and captive aspects of the study, details of which are largely given in the relevant chapters below. However, it is appropriate in this section to define terms, outline the methodological approach, and describe methods which apply to more than one aspect of the study.

2.2. Terminology: definitions and applications

CASTE. A caste is defined here partly after Wilson (1975) as a socially discrete group comprising animals of the same species, sex, reproductive condition and approximate size, and in which social rank and access to resources, including social prerogatives such as mating opportunities, are assumed to be more or less equal. The four physical determinants (above) were used to distinguish six castes for each species, namely scrotal and non-scrotal males, perforate and imperforate females, sub-adults and juveniles. The criteria used in allocating animals to castes, together with the aspects in which they were studied are given in Table 1.

The masses given in Table 1 were derived from preliminary behavioural observations, and are in total or general agreement with those obtained directly or extrapolated from the following sources: Otomys irroratus (Davis 1973); Rhabdomys pumilio (Choate 1971; Brooks 1974); Praomys natalensis (Meester 1960; Coetzee 1975; Baker & Meester 1977). Although reproductive activity may be largely restricted to animals weighing over 40g in R. pumilio (Marais

Table 1. Distinction between castes of *O. irroratus*, *R. pumilio* and *P. natalensis* recognised in the study, and aspects in which they were studied (x).

CASTE	DETERMINANTS OF CASTE				ASPECTS OF STUDY		
	Reproductive Condition	Mass			Field Studies	Captive Studies	
		O. irroratus	*R. pumilio*	*P. natalensis*		Observation	Experiment
Scrotal male	Testes fully developed and descended	90g and over	35g and over	35g and over	x	x	x
Perforate female	Vaginal orifice open	90g and over	35g and over	35g and over	x	x	x
Non-scrotal male	Testes undescended or not fully developed	90g and over	35g and over	35g and over	x	x	
Imperforate female	Vaginal orifice sealed	90g and over	35g and over	35g and over	x	x	
Sub-adult	Either sex; below minimum mass at sexual maturity, but above juvenile mass	50 - 89.9g	25 - 34.9g	25 - 34.9g	x		
Juvenile	Either sex; below minimum sub-adult mass	Under 50g	Under 25g	Under 25g	x		

1974) and P. natalensis (De Wit 1972), and in my study O. irroratus weighing under 120g were usually sexually immature, rare exceptions occurred, with apparent sexual maturity at below the specified weights. Such animals were not used in laboratory trials, and none were encountered in the field.

In addition to the information given in Table 1, a number of qualifications were applied in allocating animals to particular castes. In males, the position of the testes may vary according to temperature (Brant 1962), but those in which the testes could be stroked down into the scrotal sacs were classified as reproductive (Brooks 1974). The condition of the vaginal orifice in females (open or sealed) may not be a reliable indicator of reproductive condition as spontaneous pre-ovulatory perforation (Everett 1961) or post-copulatory fusion (Marais 1974) may occur. However, this method is generally reliable for R. pumilio (Brooks 1974), and probably for the other two species. In terms of the above definition of caste, pregnant and lactating females comprise discrete castes, but normally no attempt was made to ascertain whether free-living animals were pregnant and/or lactating since the commonly used field methods (palpation and expressing milk from the mammae respectively) are poor indicators (Measroch 1954; Brooks 1974). Although Williams & Scott (1953) did not include a sub-adult period in their definitive study, I used onset of puberty, as indicated by behavioural changes and in one case histological evidence (P. natalensis; Baker & Meester 1977), to distinguish between sub-adults and juveniles.

Where appropriate the following abbreviations are used: "scrotal" and "non-scrotal" for scrotal and non-scrotal males respectively, and "perforate" and "imperforate" for perforate and imperforate females respectively.

DYAD. An intraspecific group of two animals of any caste or castes. The term "pair" has not been used in order to avoid connotations of specifically male/female relationships.

DYADIC COMBINATION or CASTE COMBINATION. A group of analagous dyads. The six castes distinguished in Table 1 combined in diallel cross to form 21 dyadic combinations, of which 10 were studied in both observational and field studies, and 11 only in the field (Table 2).

ASSOCIATION. Presumed dyadic interaction between free-living animals.

ENCOUNTER. A period of time during which a dyad was studied in an observation cage for the purpose of quantitative analysis of social organization (Eisenberg 1967; Happold 1973, 1976). The term is not used here in the sense of a specific confrontation, as applied by ornithologists, for example (G.L. Maclean Pers. comm.).

COLONIAL and COMMUNAL. Ornithologists appear to have grounds for distinguishing between the meanings of these terms (e.g. Brown 1974), but no distinction is made here. The terms "colonial" and "communal" as used in this work are freely interchangeable, and simply indicate a high level of social cohesion in space and time.

2.3. Field studies

Field studies were undertaken from September 1976 to July 1977 at three sites in the Natal midlands, which were selected on the basis of fundamental abiotic and biotic differences among them (section 3.2.1.1). Two sites were approximately 2km apart at Dargle State Forest, Natal

Table 2. Dyadic combinations of O. irroratus, R. pumilio and P. natalensis studied both in observational and field studies (x), and in the field studies only (+).

CASTE	Scrotal male	Perforate female	Non-scrotal male	Imperforate female	Subadult	Juvenile
Scrotal male	x	x	x	x	+	+
Perforate female		x	x	x	+	+
Non-scrotal male			x	x	+	+
Imperforate female				x	+	+
Subadult					+	+
Juvenile						+

(29°28'S, 30°04'E; ± 1450m), and are here referred to as the Dargle grassland and Dargle plantation habitats. The third was at Darvill Sewage Works, Pietermaritzburg, Natal (29°37'S, 30°26'E; ± 650m), and is referred to as the Darvill habitat.

O. irroratus and R. pumilio were important members of the Dargle grassland small mammal community, but P. natalensis did not occur there. A small population of P. natalensis was present at the Dargle plantation site, along with even smaller numbers of O. irroratus and R. pumilio. P. natalensis was the most abundant species at Darvill, where O. irroratus and R. pumilio were also well represented (section 3.2.1.1).

Trapping (section 3.2.1.2) and habitat studies (section 3.2.1.3) took place concurrently, facilitating consideration of the distribution of the study species in relation to environmental factors, water (section 3.3.2) and cover availability (section 3.3.3) in particular. Trapping data (section 3.3.1) were also used to analyse the modes of dispersion of free-living O. irroratus, R. pumilio and P. natalensis (section 5).

2.4. Captive studies

O. irroratus and R. pumilio were obtained by removal-trapping at the Dargle grassland area, and P. natalensis at Darvill, or animals were progeny of stock obtained at these sites.

Observational and experimental studies were essentially discrete, although in some experiments data were acquired by direct observation, and regular observations were made of animals in all experimental situations.

2.4.1. Caging and maintenance

Animals were housed in Labotec holding cages 50 x 25 x 21cm or 50 x 25 x 10.5cm in a light controlled (14h light; 10h dark; fluorescent lighting) and partially temperature controlled (18-32°C) animal house, with coarse pine sawdust as litter and shredded paper as bedding. R. pumilio and P. natalensis were maintained on standard mouse cubes, while in addition to cubes O. irroratus were provided ad libitum with carrots and twice weekly with kikuyu grass Pennisetum clandestinum. Water was provided ad libitum. O. irroratus were caged singly, and R. pumilio and P. natalensis singly or in intraspecific pairs or larger groups depending on compatibility and availability of cages. All were toe-clipped for identification.

Animals were held captive in this way for at least one month prior to being studied in any way, and none were tested more than once in identical circumstances. After use, animals were maintained in captivity for a minimum of one month before being used again.

2.4.2. Observational studies

Observational studies were of two broad types, namely of intraspecific interaction, reported qualitatively as Social Behaviour (section 4) and quantitatively as Social Organization (section 5), and aspects of some experimental studies (section 3).

Intraspecific interaction was studied in a partially temperature (24-30°C) and humidity (65-82%) controlled observation room. A 14h light (incandescent white light)10h dark (incandescent red) light regime was

maintained, and both white and red systems were adjustable by means of variable resistors. Observation cages 120 x 60 x 60cm were glass-fronted with an external, removable nest-box 20 x 10 x 10cm at each end. Nest-boxes had clear perspex lids which were covered with cardboard when not used for observation of activities within. Cages were furnished with soil, rocks, branches and vegetation to simulate a natural environment (Eisenberg 1967; Happold 1973, 1976), but cover was sparse enough to permit constant observation of the subjects. Cages were washed using water only, and furnishings replaced prior to each trial. Food and water were provided as in the animal house, and animals were isolated and maintained in holding cages (section 2.4.1) in the observation room for one week (in addition to the minimum of one month they were maintained in the animal house; section 2.4.1) prior to study. Fur-clipping in different patterns allowed identification in dim light.

O. irroratus and P. natalensis were studied under moderate and dim red light respectively, with the white system at maximum intensity to limit activity during the simulated day. R. pumilio was studied under dim white light, with the red system adjusted to minimum intensity. The appropriate light settings for each species were ascertained during the initial stages of the qualitative study (section 4) which effectively served as a pilot study. This period also allowed me to become familiar with the social repertoires of the three species, and to decide on the duration of observation necessary to provide adequate information for the objectives of the study. Interaction was initially studied for the first four hours after introduction and for at least one hour daily for a further 14 days. However, this amount of effort was found to be relatively unproductive since interaction rates were generally extremely low after the first hour of the first day, and over 95% of social behaviour patterns were

normally utilized within five days of introduction. In addition, social relationships (e.g. hierarchical ranking) were almost invariably established by the fifth day, and thereafter adjustments were rare within the fifteen-day period. Consequently, observation time was limited to a rigidly maintained 5h/dyad for the quantitative study (section 5), while in the qualitative study (section 4) observation time averaged almost 10h/dyad, and effort was concentrated on dyads in which interaction rates were highest.

2.4.3. Experimental studies

Studies were undertaken either in the animal house, under prevailing conditions (section 2.4.1), or in a Conviron controlled environment cabinet in which light, temperature and relative humidity levels and cycles were independently adjustable (section 3.2.2).

2.5. Statistical applications

An attempt was made to quantify observations wherever possible, and to apply mathematical tests of significance. In most cases parametric tests could not be used, either because only ordinal measurement was achieved, or because the assumptions underlying their use could not be made (Sokal & Rohlf 1969). Thus, extensive use has been made of χ^2, Kruskal-Wallis one-way analysis of variance by ranks (symbolised by H), the Mann-Whitney U-test (U), and Kendall's rank correlation coefficient (τ; tau) (Siegel 1956). These are among the most powerful of the non-parametric tests, with power-efficiencies (i.e. the probability of rejecting the null hypothesis when it is false) in excess of 90% of those

of analogous parametric tests, under conditions where the assumptions associated with the statistical models of the appropriate parametric tests are met (Siegel 1956).

Parametric tests, namely the F- and t-tests, have been used in some instances, but only after the data were plotted on graph paper to ensure that their distributions were approximately normal.

Throughout this work, degrees of freedom are given as subscripts to the test symbol, except that where degrees of freedom equal one, the number is not indicated.

Single-tailed probabilities are given except where the variables were potentially dependent on one another (i.e. where the research hypothesis did not have direction; Sokal & Rohlf 1969).

3. ECOLOGY

3.1. Introduction

The questions considered in this chapter were framed in terms of the generalizations set out in the following three paragraphs.

Species adapted to the same type of habitat often have similar social organizations (Crook 1970). However, while Otomys irroratus, Rhabdomys pumilio and Praomys natalensis are frequently sympatric (section 1.2.4) the literature suggested their social systems to be fundamentally different (section 1.2.7). This suggested that niche overlap (section 1.2.5) is overshadowed by ecological differences between the three species (section 1.2.6). Such differences would be expected since available information indicated that O. irroratus is primarily mesophilous (i.e. adapted to mesic habitats), that R. pumilio is more nearly xerophilous (i.e. adapted to xeric habitats) than O. irroratus, and that P. natalensis is less nearly xerophilous than R. pumilio, but more so than O. irroratus (section 1.2.5). In addition, P. natalensis is adapted to disturbed habitats (e.g. early post-fire seres - Meester et al 1979; vegetation in which weed species are dominant - De Wit 1972; areas in the vicinity of human habitation - Coetzee 1975).

The relationship found by Barash (1974) to exist between environmental harshness (or conversely, environmental stability, expressed in terms of seasonal variation in carrying capacity) and gradients of sociability in Marmota monax, M. flaviventris and M. olympus was in effect a correlation with temperature gradients. M. monax occurs in the most stable of the habitats considered (i.e. warmest, with the longest growing season), and is the least sociable of the three species. M. olympus occurs in the

least stable habitat (i.e. coldest, with the shortest growing season), and is the most sociable; M. flaviventris is intermediate between the two extremes in respect of both sociability and habitat preference (Barash 1974). Barash (1974) predicted that there exists a general correlation between gradients of environmental stability and relative sociality in Marmota, and studies on M. caligata served to verify this prediction (Barash 1977). In her study of the social ecology of conilurine rodents in Australia Happold (1973, 1976) found xerophilous species to be generally more highly sociable than mesophilous ones. This was interpreted as reflecting differences in environmental stability, with mesic habitats more stable than xeric.

Whereas productivity and length of the growing season in temperate ecosystems are mainly limited by the physiological drought associated with extreme cold in winter (e.g. Barash 1974), seasonal water shortage may be a more important limiting factor in warmer regions such as Australia (e.g. Happold 1973, 1976) or Southern Africa. Hence, it was assumed that the social adaptations of O. irroratus, R. pumilio and P. natalensis evolved in response to the direct or indirect effects of water availability in the habitats to which these species are primarily adapted.

Well defined environmental gradients which would have facilitated description and distinction of the habitat preferences of O. irroratus, R. pumilio and P. natalensis are lacking in the Natal midlands, and there is no obvious correlation between their geographic distribution and water availability. The studies described in this chapter were thus designed largely in an sttempt to designate each species as primarily either mesophilous or xerophilous. Perrin (1981b), citing various authors, has referred to O. irroratus as inhabiting mesic habitats, and to R. pumilio

and P. natalensis respectively as having a xeric tendency and xeric tolerance.

The terms "mesic" and "xeric" are relative ones, and in the context of the generally moist Natal midlands (see section 3.2.1.1) are difficult to define precisely, especially in view of the often almost imperceptible gradation of one type into the other. In view of the high level of sympatry among the three species, and the associated difficulty of meeting the study objectives outlined above, a fine distinction between the concepts of relatively mesic and relatively xeric habitats is attempted here. For convenience, these habitat types are hereafter referred to simply as mesic and xeric. I regard as mesic a habitat with the following characteristics: water supply perennial or almost so; vegetation lush and dense, with high productivity; and growing season not limited by drought. Conversely, a xeric habitat is regarded as one in which water supply varies seasonally, causing lower vegetation density, lushness and productivity, as well as a shorter growing season, than in mesic habitats. In the Natal midlands, mesic habitats are typical of river valleys, especially river margins, and low-lying, marshy (vlei) areas, while xeric ones (as defined here) often occur on hilltops and sloping ground, and constitute much of the grassland typical of the region. An additional criterion whereby mesic and xeric habitats may be distinguished lies in the fact that xeric areas are more susceptible to fire than are mesic ones, especially during the winter, non-growing season (Pers. obs.).

Aspects selected for investigation in the present study, together with reasons for their choice and summaries of available information on the species in question, are as follows:

ECOLOGICAL DISTRIBUTION IN RELATION TO SURFACE WATER

Rationale : Primarily mesophilous species would be expected to be associated with surface water; primarily xerophilous species would not.

Available information : There is no detailed information on this subject (but see section 1.2.5).

SWIMMING ABILITY

Rationale : Primarily mesophilous species would be expected to swim more efficiently than primarily xerophilous ones. (According to G.C. Hickman In litt., who has published on swimming ability in geomyid rodents - Hickman 1977, species which live in the proximity of surface water are probably selected for greater swimming proficiency than ones which prefer drier habitats).

Available information : None.

COVER REQUIREMENTS

Rationale : In general, cover density decreases with decreasing water availability; hence, primarily mesophilous small rodents would be expected to require more dense cover than primarily xerophilous ones.

Available information : All three species occur at a wide range of cover densities, but P. natalensis appears least and O. irroratus most dependent on this factor (Meester et al 1979; Mentis & Rowe-Rowe 1979). P. natalensis appears to be a pioneer species which will

occupy an area within as little as one month of its being burnt, hence when cover density is very low (Meester et al 1979; Swanepoel 1981), and is known to migrate onto recently burnt grassland (Hanney 1965; Neal 1970; Swanepoel 1981; Lloyd In prep.). R. pumilio is generally absent for several months after fire (Christian 1977b; Meester et al 1979; Mentis & Rowe-Rowe 1979), and recolonization may take up to 12 months in montane fynbos where vegetative regeneration is slow (Willan & Bigalke In press). O. irroratus is the last of the three species to recolonize a burn, taking up to 12 months in the Natal Drakensberg (Mentis & Rowe-Rowe 1979) and two years in fynbos (Willan & Bigalke In press).

FOOD AND WATER DEPRIVATION EFFECTS

Rationale : Seasonal water shortage in xeric habitats (above) is known to inhibit primary production (Caldwell 1975), which would in turn directly or indirectly reduce the food supply of small rodents; the direct effects of scarcity of free water on obligate drinkers are self-evident. Primarily xerophilous species would be expected to display greater tolerance to food and water deprivation than primarily mesophilous ones.

Available information : None. However, Wright (1976) studied the effects of food deprivation on drinking behaviour in mesically and xerically adapted northern hemisphere rodents, and showed that during fasting xerophilous species generally exhibited absolute polydipsia (defined as water consumption at least 50% above that during conditions of ad libitum food availability), whereas mesophilous species usually decreased consumption. Despite exceptions to these trends, Wright tentatively proposed an hypothesis predicting

that drinking patterns in other mesically and xerically adapted species would prove similar to those outlined above.

In the broader context of niche separation between O. irroratus, R. pumilio and P. natalensis a number of additional investigations were undertaken. These are not described here since they were not designed to contribute directly to the main theme of this chapter (i.e. mesic vs. xeric adaptation), and will be reported elsewhere. The studies, cited as Willan (Unpubl.) in the present work, related to the distribution of free-living animals in relation to plant floristics, and to the domiciles and aspects of the feeding habits of free-living and captive animals.

3.2. Methods

3.2.1. Field studies

3.2.1.1. Study areas

Both Dargle and Darvill (section 2.3) are situated within the Southern Savanna biotic zone (Keay 1959). The two study areas at Dargle fall within Acocks' (1953) Natal Mist Belt 'Ngongoni Veld (veld type 45), and within Moll's (1965) Mistbelt Secondary Aristida junciformis Grassland. Darvill lies in a narrow spur of Acocks' (1953) Valley Bushveld proper (northern variation; type 23a), bordered to the north by 'Ngongoni Veld (type 23), and to the south by open tree Savanna, designated Southern Tall Grassveld (type 65). However, both the Dargle plantation and Darvill study areas were situated in disturbed habitats (below) and only the Dargle grassland habitat fitted the descriptions given by Acocks (1953) and Moll (1965).

The South African Weather Bureau gives the mean annual rainfall at Dargle as 988mm p.a., and at Darvill (Pietermaritzburg Municipality Weather Station at Darvill) as 823mm p.a. (Anon 1960). Mean annual temperature at Pietermaritzburg is 18.9°C (Anon 1954), from which it was estimated by D. Kopke (Pers. comm.) that the analogous value at Dargle is 15-16°C.

The main characteristics of the three habitats were as follows:

DARGLE GRASSLAND

The study area comprised a largely undisturbed grass-dominated hillside which had been planted with pines (Pinus sp.) three years previously, and adjoined an extensive stand of Mistbelt Mixed Podocarpus Forest (Moll 1965). The pines were approximately 1m tall and were insufficiently grown to have shaded out the natural vegetation. A perennial stream was present at the bottom of the hill and vegetation density, floristic diversity and lushness generally declined with increasing distance from the bank. However, a narrow firebreak (approximately 5m wide) along the edge of the stream was annually stripped of vegetation by hoeing, and the dead material removed.

DARGLE PLANTATION

The area was approximately due west of the grassland site. It was virtually level and was situated in a senescent black wattle (Acacia mearnsii) plantation in which fallen trees and rotting logs occurred, and in which considerable regeneration of wattles was taking place. A perennial stream flowed along one edge of the plantation, and a

number of narrow roads were present, largely verged by the grass Eragrostis plana.

DARVILL

The study area sloped gently (approximately 5°) and was characterized by an abundance of apparently nutrient-rich water seeping from the lowest of a series of sewage purification dams and running along shallow drainage canals. The vegetation was dominated by the exotic grass Pennisetum clandestinum, but dense stands of bullrushes Typha latifolia and an herbaceous evergreen Polygonum salcifolium were present in marshy areas. Primary productivity appeared high in this habitat, and it was perennially lush.

Table 3 lists the plant species present in the three areas. Brambles (Rubus sp.) occurring at the Dargle plantation belonged to a complex "hybrid swarm" (A.V. Hall, Pers. comm.), and could not be keyed to species. The lists were compiled from material collected in the field (section 3.2.1.3) and identified in the Herbarium, University of Natal, Pietermaritzburg. The high floristic diversity at the Dargle grassland site (70 spp., including the pines) suggested that despite afforestation the habitat was largely undisrupted. In contrast the wattle plantation represented a disturbed (disrupted) habitat in which species diversity was relatively low (25 spp., including the wattles), and in which seven other species were either exotic or are regarded as pioneers or weeds (Table 3). The Darvill habitat was also disturbed, as evidenced by the low species diversity (10 spp.), the high incidence of exotics, pioneers or weeds (seven spp.; Table 3) and domination of the vegetation by Pennisetum clandestinum, an exotic grass.

Table 3. Plant species present at the Dargle grassland, Dargle plantation and Darvill study areas. * = exotic, weed or pioneer spp.

DARGLE GRASSLAND	DARGLE PLANTATION	DARVILL
PTERIDOPHYTA		
Mohria caffrorum	Mohria caffrorum	
Pellaea viridis	Pellaea quadripinnata	
PINACEAE		
Pinus sp.*		
POACEAE		
Alloteropsis semi-alata	Agrostis bergiana	Echinochloa crus-galli*
Aristida junciformis	Aristida junciformis	Pennisetum clandestinum*
Arundinella nepalensis	Brachypodium flexum	
Cymbopogon validus	Eragrostis plana*	
Digitaria diagonalis	Eragrostis planiculmis	
Diheteropogon amplectens	Paspalum urvillei*	
Diheteropogon filifolius	Setaria sphacelata	
Eragrostis curvula	Stipa dregeana	
Eulalia villosa		
Hyparrhenia hirta		
Hyparrhenia quarrei		
Loudetia simplex		
Miscanthidium capense		
Monocymbium ceresiiforme		
Panicum ecklonii		
Paspalum dilatatum		
Pennisetum thunbergii		
Rhynchelytrum setifolium		

Continued overleaf

Table 3. Continued.

DARGLE GRASSLAND	DARGLE PLANTATION	DARVILL
Setaria sphacelata		
Themeda triandra		
Trachypogon spicatus		
CYPERACEAE		
Carex zuluensis	Carex zuluensis	Cyperus immensus
Fuirena pubescens	Cyperus albo-striatus	
Kyllinga odorata		
Mariscus sieberanus		
Scirpus costatus		
JUNCACEAE		
Juncus effusus		
TYPHACEAE		
		Typha latifolia
IRIDACEAE		
Crocosmia pottsii		
Watsonia densiflora		
AMARANTHACEAE		
	Achyranthes sicula	
ASCLEPIADACEAE		
Schizoglossum hamatum		
BORAGINACEAE		
Cynoglossum lanceolatum		

Continued overleaf

Table 3. Continued.

DARGLE GRASSLAND	DARGLE PLANTATION	DARVILL
CAMPANULACEAE		
Wahlenbergia undulata		
COMPOSITAE		
Aster bakerianus	Bidens pilosa*	
Conyza obscura	Conyza canadensis*	
Helichrysum aureo-nitens	Helichrysum aureo-nitens	
Helichrysum auriceps	Senecio deltoideus	
Nidorella auriculata	Senecio madagascariensis*	
Senecio helicopsis	Tagetes minuta*	
Senecio hygrophilus		
Senecio isatideus		
Senecio polyodon		
Vernonia natalensis		
EUPHORBIACEAE		
Acalypha peduncularis		
Acalypha punctata		
Acalypha wilmsii		
HYPOXIDACEAE		
Hypoxis angustifolia		
LAMIACEAE		
Rabdosia calycina		
LEGUMINOSAE		
Argyrolobium amplexicaule	Acacia mearnsii*	

Continued overleaf

Table 3. Continued.

DARGLE GRASSLAND	DARGLE PLANTATION	DARVILL
Argyrolobium tuberosum		
Calpurnia obovata		
Eriosema sp.		
Indigofera hedyantha		
LILIACEAE		
	Asparagus virgatus	
MALVACEAE		
Hibiscum aethopicus		
OCHNACEAE		
Hypericum lalandii		
ORCHIDACEAE		
Corycium magnum		
Eulophia calanthoides		
Satyrium longicauda		
Satyrium neglectum		
Satyrium ocellatum		
POLYGONACEAE		
		Polygonum salcifolium
PROTEACEAE		
Protea multibracteata		

Continued overleaf

Table 3. Continued.

DARGLE GRASSLAND	DARGLE PLANTATION	DARVILL
ROSACEAE		
Leucosidea sericea	*Rubus* sp.*	*Rubus cuneifolius**
Rubus ludwigii		
RUBIACEAE		
Borreria natalensis	*Conostomium natalense*	
Conostomium natalense		
Pentanisia prunelloides		
SCROPHULARIACEAE		
	Suteria floribunda	
SOLANACEAE		
		*Solanum lycopersicum**
		*Solanum mauritianum**
		*Solanum nigrum**
URTICACEAE		
		Urtica spp.*
VERBENACEAE		
Verbena bonariensis		

The locations, in relation to major features of the three habitats, of traplines on which sampling of small mammals took place, and around which habitat studies were concentrated (sections 3.2.1.2, 3.2.1.3) are shown in Figures 4 (Dargle grassland) 5 (Dargle plantation) and 6 (Darvill). Figure 4 also shows the location of a 60-station (10 x 6) grid which was trapped during the study (section 3.2.1.2). Figure 7 comprises profile diagrams of vegetation structure along the traplines, with the two Dargle grassland lines combined as a single profile, since in physiognomic terms they were not materially different.

Small mammal community structure in the three areas was ascertained by means of ad libitum trapping before commencing the studies described in section 3.2.1.2. Table 4 lists the species present in the three areas. Species diversity was highest at Darvill (11 species), and a large population of P. natalensis was present, together with smaller numbers of O. irroratus and R. pumilio. Eight species were present at the Dargle grassland, although Thallomys paedulcus, being essentially arboreal, was trapped only at the Mistbelt Mixed Podocarpus forest ecotone (Figure 4). The Dargle plantation community was depauperate judging by the presence of only four species, including a small population of P. natalensis and limited numbers of O. irroratus and R. pumilio.

Potential predators on small mammals which were identified at Dargle and Darvill are listed in Table 5. In addition, a single snake was seen at the Dargle grassland but not identified. Predatory birds were identified by Jennifer Willan, and their feeding habits ascertained from Brown & Amadon (1968) and McLachlan and Liversidge (1978). Martial and crowned eagles (Table 5) rarely take small rodents, but on three separate occasions

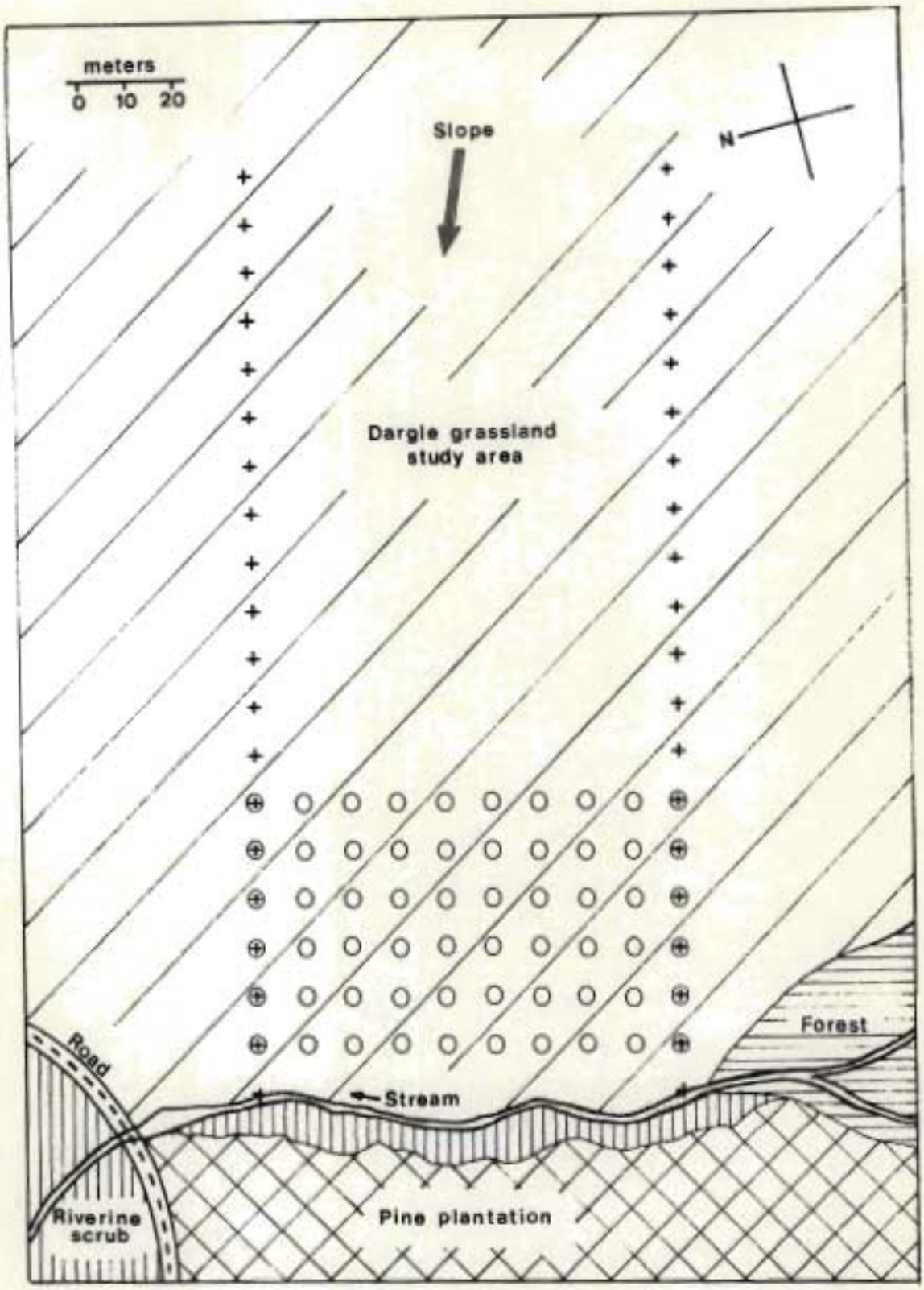

Figure 4. Location of traplines (+) and grid (O) on the Dargle grassland study area in relation to habitat.

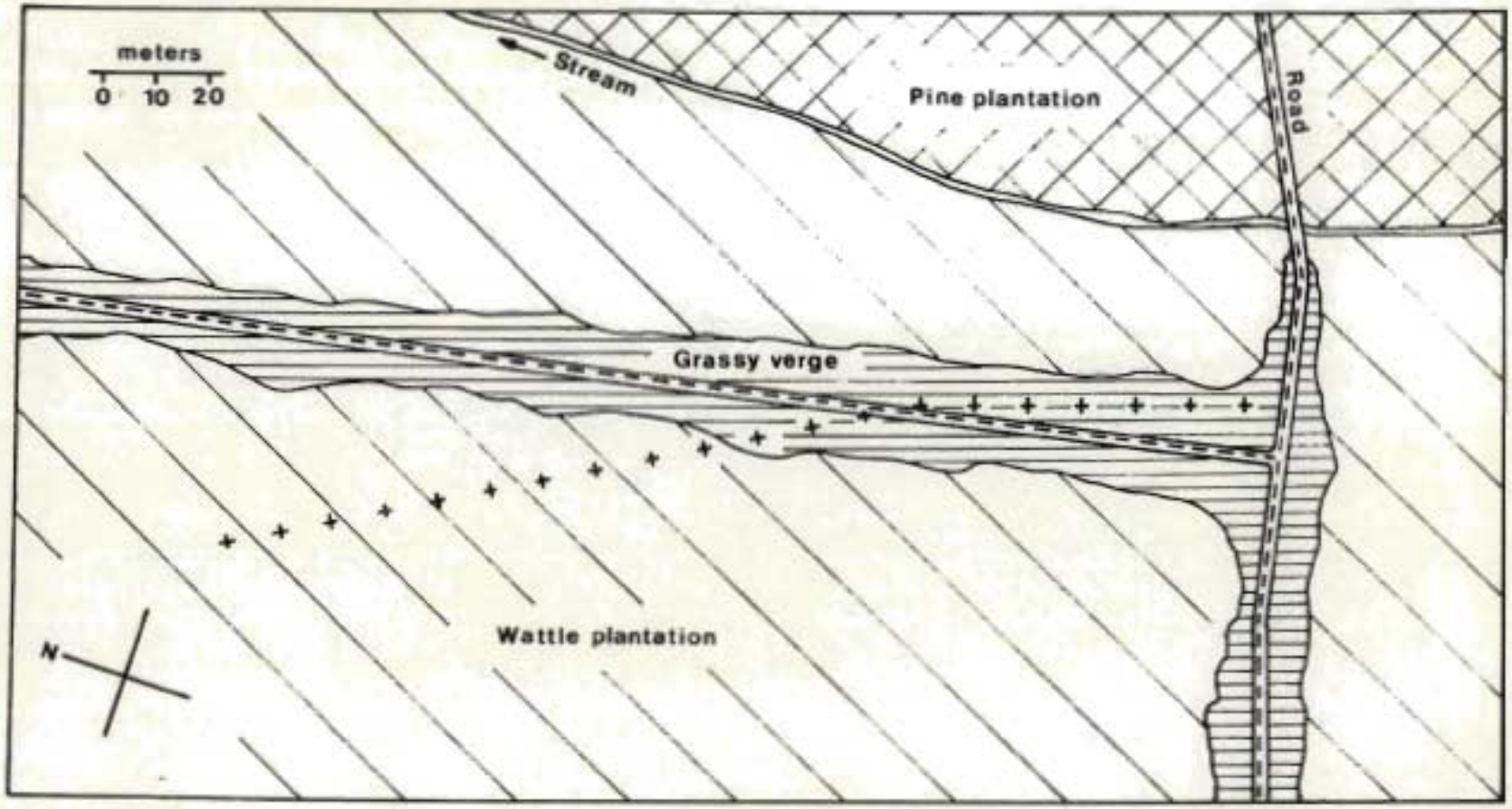

Figure 5. Location of trapline (+) on the Dargle plantation study area in relation to habitat.

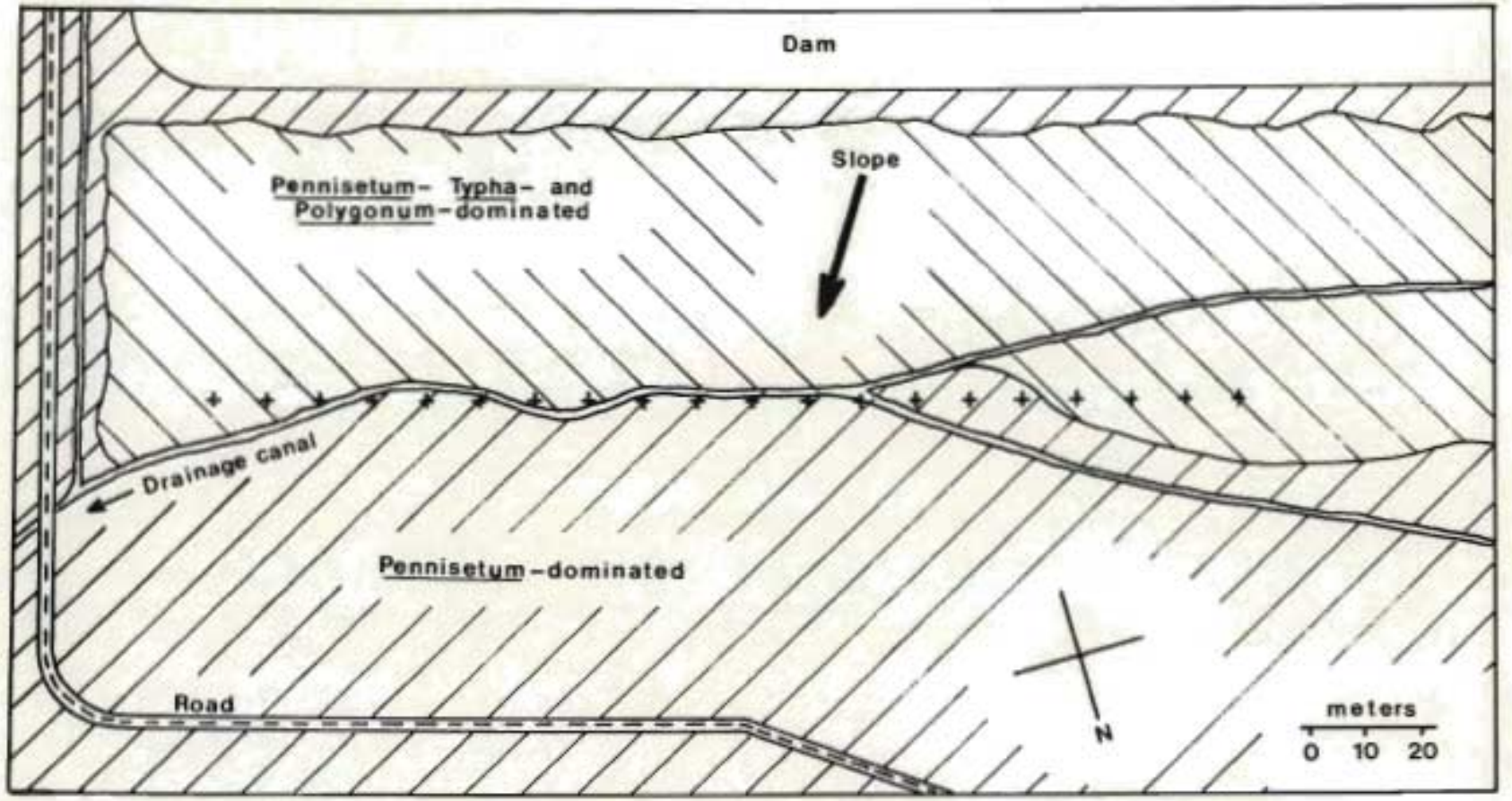

Figure 6. Location of trapline (+) on the Darvill study area in relation to habitat.

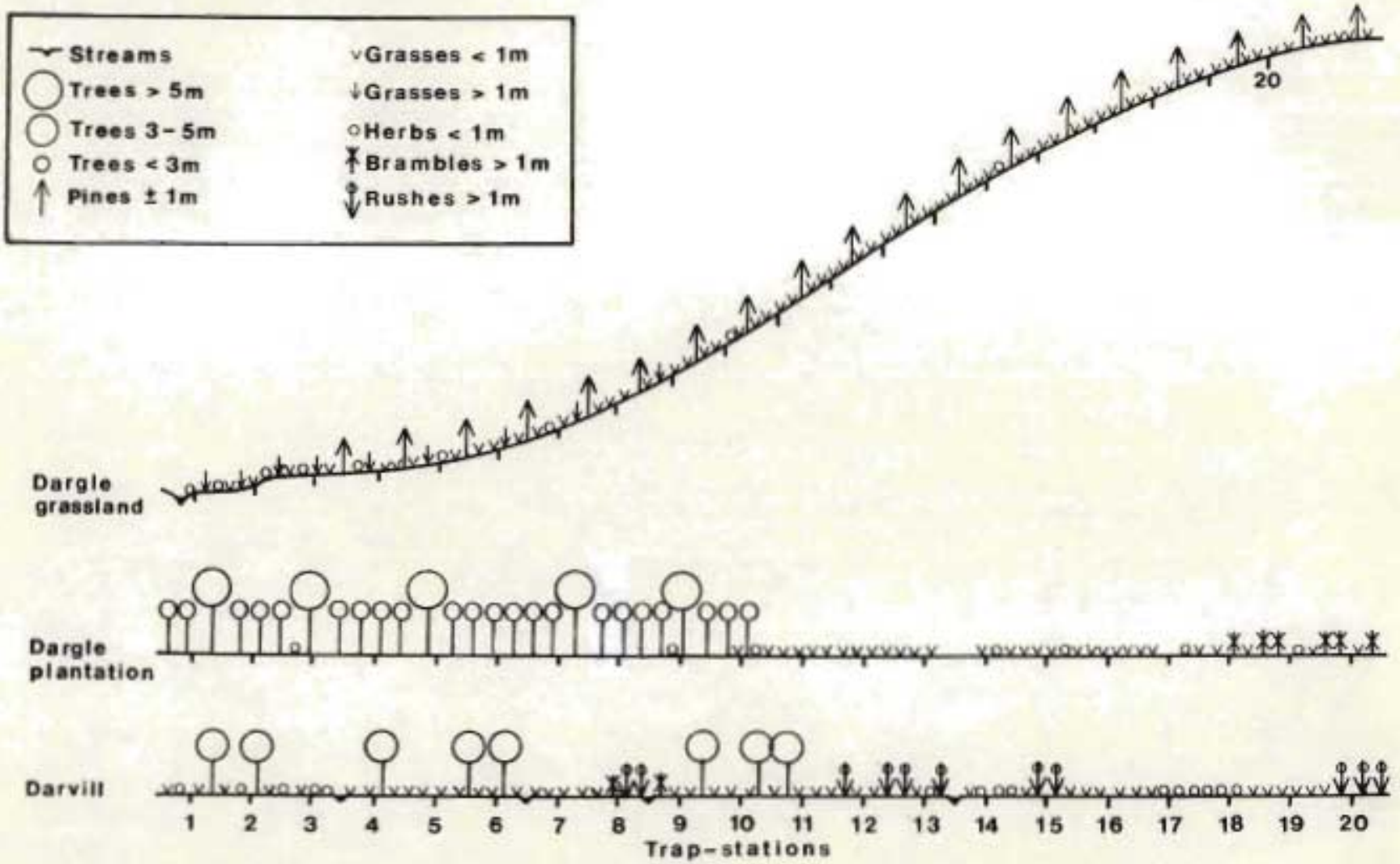

Figure 7. Profile diagrams of vegetation structure along traplines on the Dargle grassland, Dargle plantation and Darvill study areas.

Table 4. Small mammal species present at the Dargle grassland, Dargle plantation and Darvill habitats. Presence indicated by x.

SPECIES	Dargle grassland	Dargle plantation	Darvill
RODENTS			
Otomys irroratus	x	x	x
Rhabdomys pumilio	x	x	x
Praomys natalensis		x	x
Dasymys incomtus	x		x
Dendromus mesomelas	x		
Mus minutoides	x		x
Mus musculus			x
Rattus rattus			x
Thallomys paedulcus	x		
INSECTIVORES			
Crocidura flavescens	x		x
Crocidura mariquensis			x
Myosorex cafer		x	x
Myosorex varius	x		x

Table 5. Potential predators on O. irroratus, R. pumilio and P. natalensis at the Dargle grassland, Dargle plantation and Darvill study areas. Presence indicated by x.

POTENTIAL PREDATORS	Dargle grassland	Dargle plantation	Darvill
CLASS AVES			
Family Aquilidae			
Accipiter tachiro - African goshawk	x		
Buteo buteo - Buzzard	x		
Buteo rufofuscus - Jackal buzzard	x		
Elanus caeruleus - Black-shouldered kite	x		x
Polemaëtus bellicosus - Martial eagle	x		
Stephanoaëtus coronatus - Crowned eagle	x		
Family Ardeidae			
Ardea melanocephala - Black-headed heron			x
Family Bubonidae			
Bubo africanus - Spotted eagle-owl		x	
Family Scopidae			
Scopus umbretta - Hamerkop	x		
CLASS MAMMALIA			
Family Felidae			
Felis domesticus - Domestic cat (feral)	x		
Family Viverridae			
Herpestes ichneumon - Egyptian mongoose	x		

a sub-adult crowned eagle was observed to spend long periods (up to 2h) perched at the forest fringe at the Dargle grassland site (Figure 4), apparently seeking prey in the adjoining grassland.

3.2.1.2. Trapping studies

Four types of traps were available: hardboard live-traps 270 x 90 x 85mm (Meester 1970), PVC live-traps 216 x 68 x 54mm (Willan 1979), and Museum Special and large (rat) snap-traps. During the course of the present study the relative efficiencies of hardboard and PVC traps were tested, and they were found to be complementary, with PVC traps more efficient for very small animals, and hardboard traps for larger ones (Willan 1979; Appendix 3). Both of these trap types have transparent perspex rear doors, and the results of a later study (Willan In prep.) led to the conclusion that this feature may increase trap efficiency for O. irroratus and R. pumilio, while not reducing efficiency for other species. Traps were baited with a rolled oats/raisin mixture, following a limited trial during pilot trapping at the Dargle grassland site in which this bait provided generally higher catches than oats/peanut butter. The choice of this bait was later proved to be justified in more comprehensive trials in which oats/raisins was shown to be relatively highly efficient, and oats/peanut butter relative inefficient (Willan In prep.). Pre-baiting was not employed as its effects are poorly understood (see Flowerdew 1976).

Debris was removed from traps whenever necessary, but traps were never washed, either during or between trapping sessions. Little is known of the effects of trap odour, but olfactory cues appear to influence trappability of at least some species (Rowe 1970; Boonstra & Krebs 1976), generally

with a positive correlation between capture rate and presence of conspecific odour. This appears to be the case in R. pumilio (C.N.V. Lloyd Pers. comm.), but in contrast overall trap efficiency may be reduced by the odour of P. natalensis (C.N.V. Lloyd Pers. comm.) or C. flavescens (D.T. Rowe-Rowe Pers. comm.). Consequently, there can be no certainty that the practice of not washing traps influenced their efficiency either way, but since odours dissipate with time it is unlikely that the results of discrete trapping sessions, which were usually a month apart, were influenced by trap odour.

Additional invariable aspects of trapping methodology (except during ad libitum trapping, below) were as follows:

1. The distance between trap-stations was 10m.
2. Traps were set within 1m of station-markers, abutting runways if these were present.
3. Traps were cleared morning and evening (approximately sunrise and sunset).
4. An excess of traps was provided at every station, evidenced by the fact that in less than 2% of cases were all traps occupied at a particular station at the same time. Since the number of traps/station varied according to local abundance of small mammals, data are interpreted in terms of "station-nights" rather than "trap-nights". This was done to provide indices of relative abundance (section 3.3.1) which, irrespective of the number of traps/station, were directly comparable as between species and sites.

Details of trapping procedures are given in Table 6. The bulk of trapping comprised removal trapping on traplines, but during the capture-mark-recapture (CMR) procedure, animals were released at the point of capture after having been marked using the 1-2-4-7 toe-clipping method. Animals were in all cases weighed and sexed, and their reproductive condition was noted, together with the time, place and other conditions of capture (e.g. trap-type). Ad libitum snap-trapping of habitats other than those referred to above was undertaken at Dargle during September 1976 - January 1977. This was done largely in an effort to locate a P. natalensis population which could be monitored simultaneously with the Dargle grassland community. However, the only population located (in the wattle plantation) proved too small to warrant major sampling effort.

O. irroratus and R. pumilio live-trapped on the Dargle grassland lines, and P. natalensis from Darvill, were removed to the laboratory for experimental and observational study. P. natalensis live-trapped at the plantation site were removed to the laboratory but were not used in the present study.

Study skins were prepared of representative samples of all three species from both Dargle and Darvill, and lodged in the Department of Zoology, University of Natal, Pietermaritzburg. All animals handled during the study were examined for ecto-parasites, and snap-trapped specimens for endo-parasites as well. Parasites were preserved in 4% formaldehyde solution and lodged in the Natal Museum, Pietermaritzburg.

Trapping at Dargle was discontinued after May 1977 when it became obvious that population densities, which had been expected to rise in autumn (O. irroratus - Davis 1973; R. pumilio - Brooks 1974; P. natalensis

Table 6. Methods used to sample O. irroratus, R. pumilio and P. natalensis* at the Dargle grassland, Dargle plantation and Darvill study areas. Traps: H = hardboard; P = PVC; M = museum special.

PARAMETERS	DARGLE GRASSLAND		DARGLE PLANTATION	DARVILL
	Traplines	Grid	Trapline	Trapline
Type of trapping	Removal	CMR	Removal	Removal
Number of stations	20x2=40	10x6=60	20	20
Traps/station	3(H,P,M)	2(H,P)	3(H,P,M)	6(3H,3P)
Nights/station/month	3 (3 days, 3 nights)	7 (7 days, 7 nights)	3 (3 days, 3 nights)	3 (3 days, 3 nights)
Station-nights/month	120	420	60	60
Months sampled	8 (October 1976-May 1977)	1 (January 1977)	3 (March-May 1977)	2 (April, May 1977)
Total station nights	960	420	180	120
(Total trap-nights)	(2880)	(840)	(540)	(720)

* P. natalensis absent from Dargle grassland habitat

- Coetzee 1965), were too low to warrant further sampling. Trapping at Darvill was discontinued at the same time, since a sufficient number of captures had been made of P. natalensis to permit comparison with available data on O. irroratus and R. pumilio from the Dargle grassland study area. On account of the small sample sizes monthly data were summed for each site, and interpretation of trapping results is based on mean densities and overall distributions. Consideration of seasonal variation in environmental parameters is thus also omitted (section 3.2.1.3).

3.2.1.3. Habitat utilization studies

The presence of shallow (up to 5cm) standing water occurring within 5m of station-markers at Darvill was charted on graph paper and scored according to the scale:

0 = no standing water

1 = up to 5% of the area water-covered

2 = >5% of the area water-covered

Relative cover density at each trap-station (section 3.2.1.1) was ascertained by measuring light penetration to ground level using a light-dependent resistor (LDR Phillips 2322 600 93001) attached to a 60cm probe and coupled to an ohmeter. In the vicinity of some stations at Darvill, Solanum mauritianum (a small tree 3-5m in height) formed a partial canopy which was insufficiently dense to occlude lower-growing vegetation (section 3.2.1.1). Where light readings were taken under vegetation shaded by the trees, the value obtained under the trees alone was also recorded. A similar procedure was followed in respect of Acacia mearnsii at the Dargle plantation. During each trapping session (section 3.2.1.2) and in July

1977, 10 readings were taken within 5m of each station-marker, in small mammal runways when possible, and always on cloudless days between 12h00 and 14h00. Data for each station were summed for all months, and station means calculated. These were based on the following numbers of readings/ station: Dargle grassland 90; Dargle plantation 40; Darvill 30. An inverse linear relationship exists between light intensity and resistance of LDR's (i.e. readings in ohms decrease as light intensity increases). Hence, low readings were correlated with low vegetative cover (i.e. high light penetration) and vice versa. Thus, although a curve is given for conversion of ohms to lux (the S.I. unit of light intensity) (Figure 8), derived by calibration of the LDR-ohmeter device against a lux meter, light penetration data are presented as ohms.

3.2.2. Experimental studies

The source of animals used in laboratory studies and details of their confinement prior to experimentation are given in section 2.4.

Responses to substrate moisture and cover availability were tested in the animal house (section 2.4.3) in a choice chamber apparatus consisting of four plexiglass boxes 30 x 25 x 25cm, linked in horizontal series by 10cm lengths of 5cm plexiglass tubing located 1cm from the bottom of the boxes. Each chamber was fitted with a removable timber-framed gauze lid, and a food dish and calibrated water bottle were attached to one wall. Before all trials the apparatus was dismantled and washed in hot water; thereafter approximately 1kg of fine, clean, dry sand was spread about in each chamber, and nesting material (shredded paper) and ad libitum food (crushed mouse cubes, plus carrot in the case

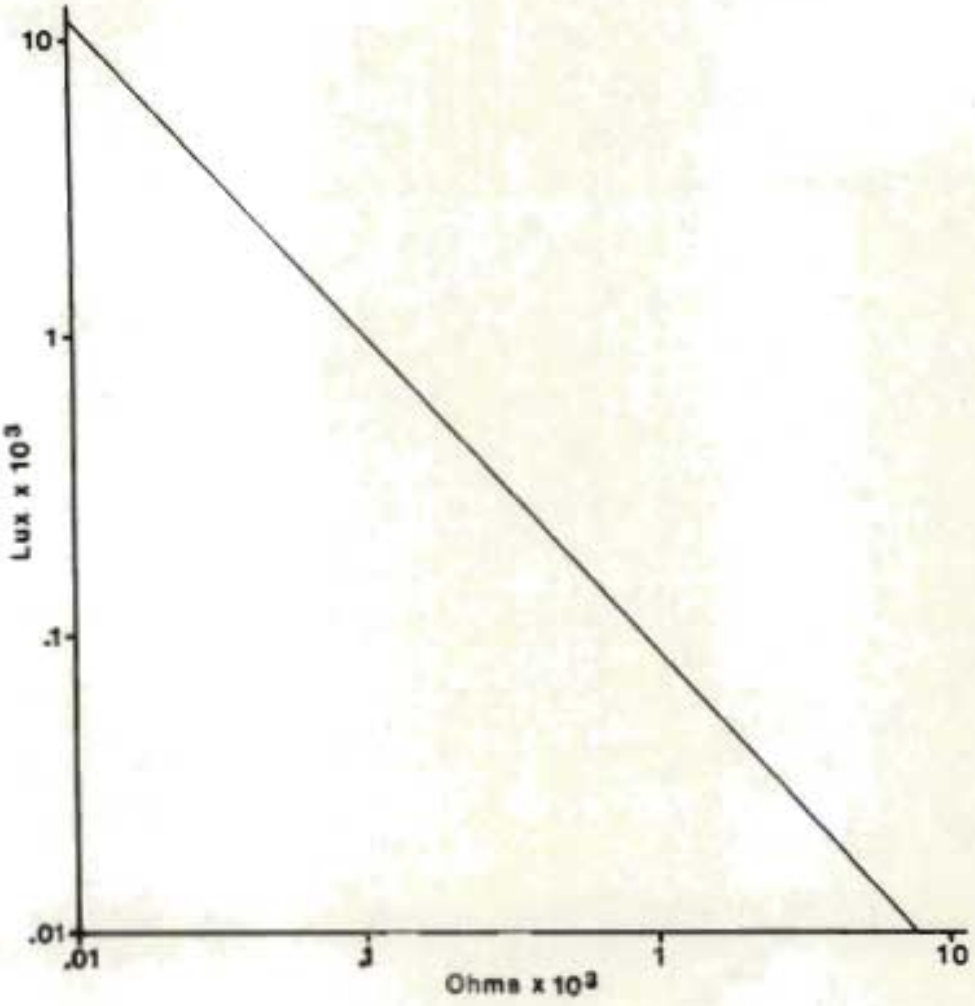

Figure 8. Calibration curve for conversion of ohms to lux.

of O. irroratus) and water were provided. Food was weighed and available water was recorded before commencement of each trial. Responses to two sets of conditions (i.e. high and low cover, and wet and dry substrate; below) were tested separately by providing differing environments in alternate chambers. Animals were individually placed in the apparatus and left for 24h. Utilization of each chamber was measured in terms of food and water consumption, faeces deposition, and nest construction. Twenty animals (10 males, 10 females) of each species were tested under each set of conditions, although in an initial series of calibration tests, half that number were used. Additional details of methods were as follows:

Initial calibration. The chambers were identically furnished (above), and animals did not discriminate between them in terms of the parameters measured.

Substrate moisture. Water (about 300ml) was added to the sand in two of the chambers, either the odd- or even-numbered ones in a series numbered 1-4.

Cover availability. Heavy black cloth was draped over the odd- or even-numbered chambers.

Swimming ability of 20 animals (10 males, 10 females) of each species was studied in the animal house (section 2.4.3) following the method described by Hickman (1977). Tests were conducted in a 25l polythene bucket filled to a depth of 30cm with water (23°C at the commencement of each trial). Animals were tested individually. They were held by the scruff of the neck, gently lowered into the water, and released when

apparently buoyant. Care was taken not to drop them to avoid unnecessarily wetting the fur. Swimming behaviour was noted throughout each trial, and duration of swimming recorded to the nearest minute. A trial was terminated by removing the animal from the water when its nostrils first submerged, since it was then in danger of drowning (Hickman 1977). Brief submergence of the nostrils during initial panic when an animal was first placed in the water was ignored. The selected endpoint (i.e. first submergence of the nostrils) may be regarded as subjective, but drowning the animals was undesirable. In addition, the animals were so weakened by the time the endpoint was reached that they would apparently have drowned soon thereafter.

The effects of food deprivation on body mass and water consumption, and of water deprivation on body mass and food consumption in the three species were ascertained in holding cages 50 x 25 x 21cm (section 2.4.1) in a controlled environment cabinet (section 2.4.3). In all experiments the light cycle was 14h light, using the fluorescent lighting system set at high intensity, and 10h dark. With the exception of trials in which the responses of R. pumilio and P. natalensis to water deprivation under harsh environmental conditions were tested (below), temperature and relative humidity were respectively 25°C/50% RH during the light period and 15°C/70% RH during the dark. This regime was designated "standard". Harsh environmental conditions, which were assumed to approach those obtaining in arid environments such as the S.W. Arid, were respectively 35°C/20% RH and 15°C/70% RH during the light and dark periods. A thermohygrograph placed in the cabinet for one week under each regime showed the delay in temperature adjustment from one part of the cycle to the next to be approximately 10 minutes, and in relative humidity approximately 35 minutes under standard conditions. Under harsh conditions

adjustment of both temperature and relative humidity took approximately twice as long. Each cage was equipped with a plastic feeding dish and calibrated drinking bottle, but litter and bedding were not provided during deprivation experiments since animals, particularly R. pumilio, were found to ingest both sawdust and paper (section 2.4.1) during starvation. However, sections of PVC downpipe of the type used to construct PVC traps (Willan 1979) were provided in which animals were able to take cover. The cabinet was able to hold eight cages, and two replications/species were run in which either males or females were tested. The sexes were separated to avoid the possibility of sex-related odours influencing the results. Each run was preceded by a period of one week's acclimatization during which food and water were supplied ad libitum. This was followed by a further ad libitum period, an experimental (deprivation) period, and a final recovery period, during all of which ingestion and body mass were recorded every 24h. The foods of the three species during deprivation experiments were the same as those provided under holding conditions (section 2.4.1), except that O. irroratus was not supplied with kikuyu grass. To facilitate comparison of food consumption in O. irroratus with that in the other two species the energy values of mouse cubes and carrot were ascertained using standard bomb calorimetry, and the mass of food ingested converted to its energy equivalent. Only crude comparison was possible, however, since the physiological fuel values of the two foods were not investigated.

Activity of the three species in relation to food deprivation was studied under standard conditions in the controlled environment cabinet (above). In the case of R. pumilio and P. natalensis activity wheels were constructed to fit into holding cages 50 x 25 x 21cm (section 2.4.1). The wheels were 471mm in circumference, and were constructed of 80mm-wide pieces of 10mm welded wire mesh set 5mm from the edge of plexiglass

discs 155mm in diameter. The wheels rotated on metal spindles set into plexiglass backing-boards, to each of which was attached a microswitch that was activated at every revolution by a metal pin set into the back of the wheel. The microswitches were connected via a port in the cabinet wall to a battery of externally located electronic counters. O. irroratus was found to be too large to use these wheels, and an apparatus comprising a larger (765mm circumference) activity wheel with attached cage and mechanical counter was used. The general method, including provision of food and water, was the same as for the deprivation experiments described above, except that in the case of O. irroratus 16 replications were necessary to provide sufficient data for comparison with those for the other two species. The counters were read every 24h, and the number of revolutions converted to km/h.

In order to standardize the above deprivation experiments, consideration was given to running them until the animals died. However, as in the case of swimming trials (above), this was regarded as undesirable; moreover, information was required on recovery rates following deprivation (above). When possible, deprivation was terminated before any animals died, when their condition was such that further deprivation would apparently have resulted in mortality within a period of 12h. This endpoint may be regarded as subjective, but animals were generally so weakened by the time trials were terminated that they were incapable of efficient locomotion. In the absence of food or water (depending on the circumstances), free-living animals in such condition would not be expected to live for more than a few hours, and the maximum tolerances to deprivation recorded in this study (section 3.3.4) probably reflect the field situation quite accurately. Furthermore, there were gross differences in the tolerances to deprivation of the three species (section 3.3.4), and it is highly

unlikely that selecting a different endpoint would have materially influenced the conclusions reached in this regard (sections 3.4.3, 3.4.4.1).

3.3. Results

3.3.1. Trapping data

Ninety-two individual O irroratus, 159 R. pumilio and 275 P. natalensis were trapped during the study (Table 7). Numbers at Dargle (both sites) were too low to warrant estimation of relative population densities by the removal method (Southwood 1966), and percentages of trapping success/ station-night of effort were thus calculated to provide indices of relative abundance in the three areas (Table 7). The results of trapping on traplines at the three sites are comparable in view of the similarity in sampling methods (section 3.2.1.2). Population densities of all three species were apparently higher at Darvill than at either of the Dargle sites (Table 7).

The distribution of O. irroratus, R. pumilio and P. natalensis on the traplines is illustrated in Figure 9.

3.3.2. Water

3.3.2.1. Distribution of free-living animals in relation to water

On the two traplines at the Dargle grassland, station 1 was at the edge of the stream, while station 20 was 190m from the stream (section 3.2.1.1). At Darvill, standing water was present as follows:

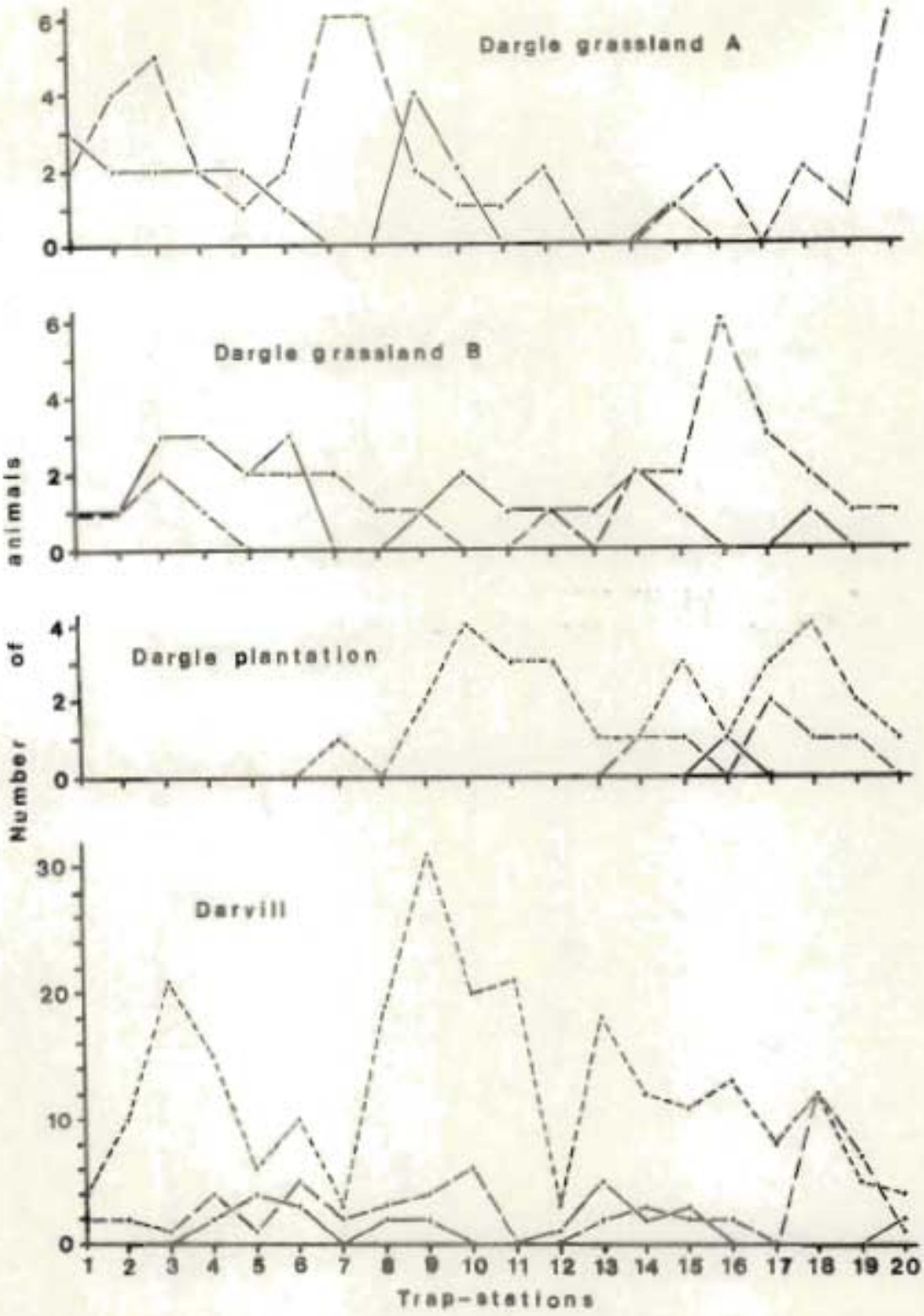

Figure 9. Distribution of O. irroratus (——), R. pumilio (— —) and P. natalensis (----) on the Dargle grassland (traplines A and B), Dargle plantation and Darvill study areas.

Table 7. Numbers of O. irroratus (O), R. pumilio (R) and P. natalensis (P) captured at the Dargle grassland, Dargle plantation and Darvill study areas. n = number of animals; % = per cent trapping success/station-night of effort.

MONTHS	DARGLE GRASSLAND								DARGLE PLANTATION						DARVILL					
	Traplines				Grid				Trapline						Trapline					
	O		R		O		R		O		R		P		O		R		P	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
October 1976	1	0.8	9	7.5																
November	1	0.8	10	8.3																
December	15	12.5	6	5.0																
January 1977	6	5.0	8	6.7	23	8.9*	19	7.2*												
February	9	7.5	9	7.5																
March	2	1.7	6	5.0					-	0	2	3.3	15	25.0						
April	5	4.2	17	14.2					-	0	3	5.0	10	16.7	11	18.3	23	38.3	104	173
May	3	2.5	10	8.3					1	1.7	1	1.7	4	6.7	15	25.0	36	60.0	142	236
TOTALS	42	4.4	75	7.8	23	8.9*	19	7.2*	1	0.6	6	3.3	29	16.1	26	21.7	59	49.2	246	205
MALES	19		40		12		11		1		4		13		14		33		119	
FEMALES	23		35		11		8		0		2		16		12		26		127	

* Calculated for total animals caught in first three nights

Stations	Score	Descriptions
4 - 11	0	No standing water; "dry"
13 - 16	1	Up to 5% water-covered; intermediate
1-3; 12; 17-20	2	More than 5% water-covered; marshy

The distribution of O. irroratus at the Dargle grassland was negatively correlated with increasing distance from the stream, and P. natalensis was negatively associated with standing water at Darvill (Table 8).

3.3.2.2. Responses of captive animals to substrate moisture

Table 9 summarizes the results of choice-chamber responses (section 3.2.2) of 20 animals (10 males, 10 females) of each species to wet and dry substrates.

O. irroratus and R. pumilio constructed significantly more nests in dry chambers than in wet, but P. natalensis did not discriminate (Table 9). Fewer animals moved nesting material between chambers than occurred when responses to cover were tested in the same apparatus (section 3.3.3.2), with a single R. pumilio and two P. natalensis approximately doubling the amount of material in the chamber in which their nests were built (R. pumilio in a dry chamber; P. natalensis, one wet and one dry).

3.3.2.3. Swimming ability of captive animals

A qualitative account of swimming ability and behaviour in the three species is given in Table 10. Males and females are not distinguished since there were no apparent differences between the sexes.

Table 8. Regression analysis (Kendall's τ) of the distribution of O. irroratus, R. pumilio and P. natalensis in relation to water at the sites indicated. N = number of trap-stations; τ = Kendall's tau statistic; z = normal distribution statistic; P = statistical significance; c = correlation; -ve = negative.

SPECIES	DISTANCE FROM WATER				STANDING WATER			
	Dargle grassland (N=40)				Darvill (N=20)			
	τ	z	P	c	τ	z	P	c
O. irroratus	-.469	-4.15	<.00003	-ve	-.244	-1.51	.0655	
R. pumilio	+.085	+0.75	.2266		-.246	-1.52	.0643	
P. natalensis					-.364	-2.24	.0125	-ve

Table 9. Intraspecific analysis (Student's t; χ^2) of the responses of captive O. irroratus, R. pumilio and P. natalensis to substrate moisture, measured in terms of food and water consumption, and numbers of faecal pellets deposited and nests constructed in wet and dry chambers respectively. P given where values of t and χ^2 were less than the 5% level of significance.

SPECIES	PARAMETERS															
	$\bar{X}$ Food (g)				$\bar{X}$ Water (ml)				$\bar{X}$ Faeces (number)				Nests (total)			
	wet	dry	t_{19}	P	wet	dry	t_{19}	P	wet	dry	t_{19}	P	wet	dry	χ^2	P
O. irroratus	21.5	33.2	1.71		4.4	5.0	1.53		40.2	30.1	0.97		2	19	13.76	<.001
R. pumilio	2.4	1.8	2.08		5.0	5.6	0.73		20.1	25.0	1.49		2	12	7.14	<.01
P. natalensis	2.2	1.9	0.87		3.7	4.2	0.79		14.0	16.3	0.43		9	11	0.20	

Table 10. Swimming behaviour of captive *O. irroratus*, *R. pumilio* and *P. natalensis*.

PARAMETERS	COMMON TO ALL	*O. irroratus*	*R. pumilio*	*P. natalensis*
INITIAL REACTION	Frantic (panic) swimming, with attempts to climb out of bucket.	Lasting ± 1 minute.	Lasting ± 3 minutes.	Lasting 2-5 minutes.
BODY POSITION	Angle from horizontal increasing with time.	Body initially at ± 30° from horizontal, with angle gradually increasing until almost vertical (usually when about two-thirds of duration of trial had elapsed). Body mass largely supported by "ruff" of unwetted hair around neck - inclination increasing as area of "ruff" reduced by wetting.	Initially horizontal (first 3-5 minutes), but inclining at ± 45° from horizontal when initial frantic swimming ceased. Ears submerged during this (± 45°) stage. Body almost vertical during last 5-10 minutes, with nostrils just clear of surface.	Body initially at ± 30° from horizontal, but angle increasing to ± 60° within 15 minutes, and remaining at about that inclination thereafter. Body mass largely supported by "ruff", as in *O. irroratus*, and inclination increasing with decreasing area of ruff.
LOCOMOTION	Initial vigorous movements of all four limbs and undulation of tail. Thereafter, effort reduced.	After initial reaction, effort reduced to ± 10% of initial effort, with only occasional movements of limbs and tail. Limbs moved directly under body in motion analogous to running. Periods of up to 1 minute spent floating with no limb or tail movements.	After initial reaction, effort reduced to ± 25%, but further reduced to ± 5% during last 5-10 minutes. Limbs moved directly under body, as in *O. irroratus*. Swimming attempts largely ineffectual during last few minutes (about one-third of duration) when body almost vertical.	Little attempt to swim after initial reaction, with effort reduced to ± 10%. However, when utilized, limb movements and tail undulation stronger than in other two species. Fore-limbs moved directly under body, but hind limbs held further out and used in strong sculling motion. Long periods (up to 3 minutes) spent floating.
VOCALIZATION		None audible.	Animals often squeaked during stage when body at 45°.	None audible.

Mean swimming duration (minutes) was not significantly different between the sexes in R. pumilio (males 15.0; females 16.4; $t_{18} = 0.56$; $P>.05$) and P. natalensis (males 31.6; females 35.8; $t_{18} = 1.18$; $P>.05$), but O. irroratus females (31.9) were able to swim for significantly longer than males (21.2) ($t_{18} = 3.09$; $P<.01$). Consequently, in statistically comparing mean swimming duration in these species (Table 11), data for male and female O. irroratus are treated separately, but are combined for the two sexes of R. pumilio and P. natalensis.

Swimming ability was significantly greater in both male and female O. irroratus and in P. natalensis, than in R. pumilio, but whereas P. natalensis endured for significantly longer than O. irroratus males there was no significant difference in respect of females (Table 11).

3.3.3. Cover

3.3.3.1. Distribution of free-living animals in relation to cover

At the Dargle grassland, station 1 on traplines A and B fell within the 5m-wide firebreak (section 3.2.1.1), where cover density increased rapidly with time following the previous clearing. These stations are thus dealt with separately from the remainder. At all other stations at the three sites, cover density remained approximately constant during all months sampled.

Distribution of cover at the three sites is illustrated in Figure 10.

O. irroratus was positively associated with high cover density on the Dargle grassland, but this factor did not significantly influence its

Table 11. Interspecific analysis (Student's t) of mean swimming duration (minutes) of captive O. irroratus, R. pumilio and P. natalensis. P given where values of t were less than the 5% level of significance.

O. irroratus		R. pumilio	P. natalensis	Statistics
Males	Females			
21.2		15.7		t_{28} = 2.69; P<.01
	31.9	15.7		t_{28} = 5.74; P<.001
21.2			33.7	t_{28} = 4.53; P<.001
	31.9		33.7	t_{28} = 0.54
		15.7	33.7	t_{38} = 8.20; P<.001

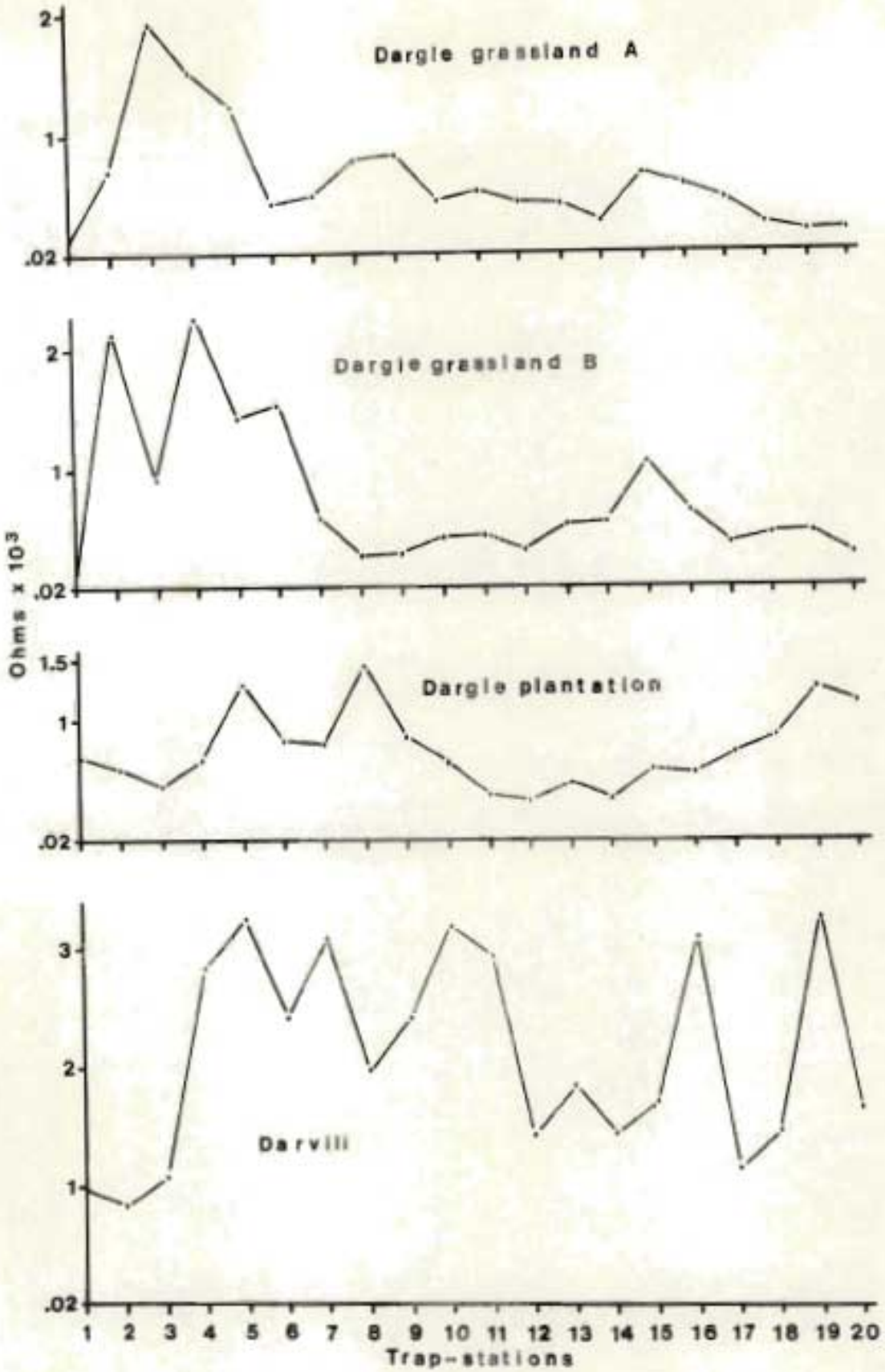

Figure 10. Distribution of cover at the Dargle grassland (traplines A and B), Dargle plantation and Darvill study areas. .02 x 10^3 ohms = reading in full sunlight.

distribution at Dargle (Table 12), where available cover was in excess of its apparent minimum requirements (below). However, cover density on the Dargle grassland was negatively correlated with distance from the stream ($\tau = -.454$; $z = -4.01$; $P<.00003$). Together with the negative association of O. irroratus with distance from the stream (section 3.3.2.1), this suggests the distribution of this species to have been determined by an interrelated cover/distance from water complex. Comparison of values of τ for the distribution of O. irroratus in relation to cover (Table 12) and distance from water (section 3.3.2.1) permits the tentative conclusion that the effects of these two variables were almost indistinguishable (Siegel 1956). In general O. irroratus appeared to favour dense cover close to water, although its distribution may have been independently determined by either of these factors, and not by the combined effects of both.

The distribution of R. pumilio on the Dargle grassland and at Darvill, and of P. natalensis at the two sites where it occurred, was not significantly influenced by cover availability (Table 12).

Although the distribution of P. natalensis in the Dargle plantation was not correlated with that of overall cover density as measured in this study (Table 12), consideration of cover exclusive of that provided by the wattles showed this species to have been strongly associated with ground cover, which was practically absent from the plantation proper ($\tau = +.549$; $z = 3.38$; $P<.00005$).

Four O. irroratus and three R. pumilio were trapped on the Dargle grassland firebreak (station 1; traplines A and B combined; Figure 9), which had been denuded of vegetation during September 1976, the month

Table 12. Regression analysis (Kendall's τ) of the distribution of O. irroratus, R. pumilio and P. natalensis in relation to cover density at the sites indicated. N = number of trap-stations; τ = Kendall's tau statistic; z = normal distribution statistic; P = statistical significance; c = correlation; +ve = positive.

COVER DENSITY	O. irroratus				R. pumilio				P. natalensis			
	τ	z	P	c	τ	z	P	c	τ	z	P	c
Dargle grassland (N = 38)	+.447	+3.95	<.00005	+ve	+.075	+0.67	.2514					
Dargle plantation (N = 20)									-.036	-0.22	.4219	
Darvill (N = 20)	+.109	+0.67	.2514		+.241	+1.49	.0681		+.096	+0.59	.2776	

prior to commencement of sampling. These numbers of animals were similar to those for the adjoining stations (2A, 2B), where mean cover density was approximately 10 times as high as at station 1 (Figure 10). The first M. pumilio was trapped on the firebreak when aerial cover was negligible, but O. irroratus did not appear until light penetration to ground level had fallen to approximately 275 ohms (343 lux) (Figure 11). Elsewhere on the traplines O. irroratus did not occur at stations where light penetration was greater than 285 ohms (330 lux) (Figures 9, 10), and these values (about 340 lux) may approximate the upper limit of light tolerance of this species. The firebreak was again cleared in June 1977, and was trapped ad libitum the following month (40 station-nights), without success.

3.3.3.2. Responses of captive animals to cover availability

The results of cover response (choice-chamber) trials (section 3.2.2), representing mean values for 20 animals (10 of either sex) of each species, are given in Table 13. During the daylight part of the light cycle (section 3.2.2) light intensity, measured with the LDR-ohmeter device used in the field (section 3.2.1.3), was approximately 3200 ohms (23 lux) in the darkened (cloth-covered) chambers, and approximately 450 ohms (198 lux) in the ones which were not covered. These values were respectively similar to those in areas of high and low cover density in the field (section 3.3.3.1).

All three species constructed significantly more nests in high-cover than low-cover chambers (Table 13). O. irroratus in addition consumed a significantly larger proportion of its food in high-cover than in low-cover chambers, while P. natalensis deposited significantly more faeces in low-cover than in high-cover ones (Table 13).

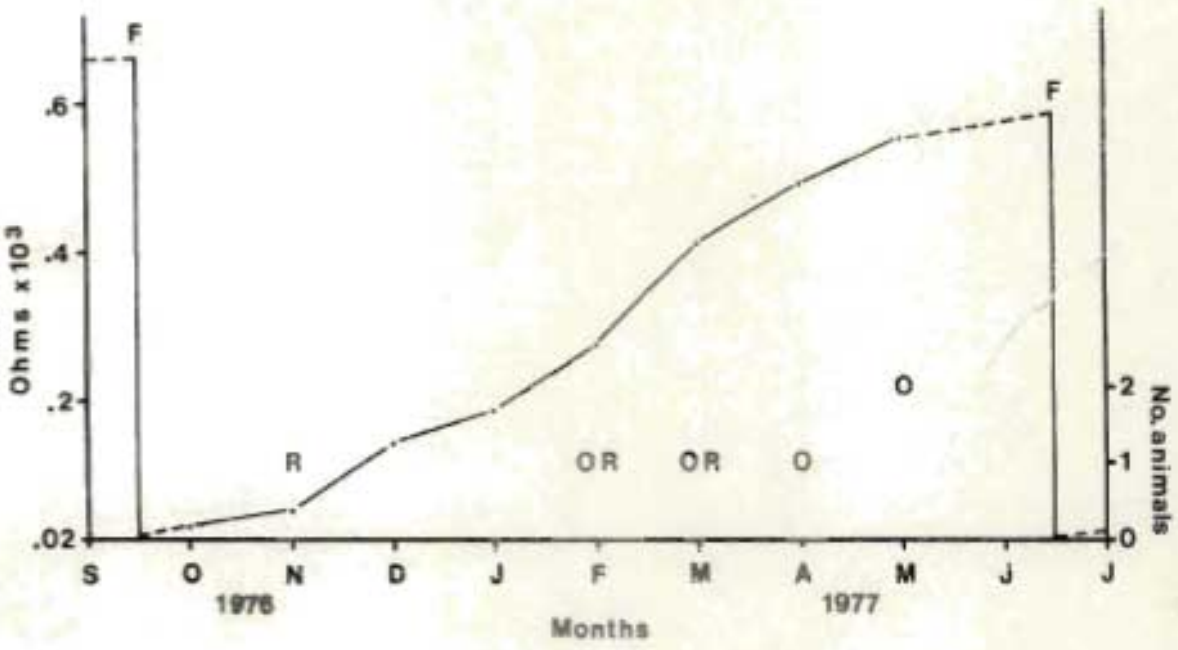

Figure 11. Recolonization by O. irroratus (O) and R. pumilio (R) and increase in cover (——) following removal (F) of vegetation from a firebreak at the Dargle grassland study area. Broken lines: assumed approximate cover densities; .02 x 10^3 ohms = reading in full sunlight.

Table 13. Intraspecific analysis (Student's t; X^2) of the responses of captive O. irroratus, R. pumilio and P. natalensis to cover availability, measured in terms of food and water consumption, and numbers of faecal pellets deposited and nests constructed in high- and low-cover chambers respectively. P given where values of t and X^2 were less than the 5% level of significance.

SPECIES	PARAMETERS															
	$\bar{X}$ Food (g)				$\bar{X}$ Water (ml)				$\bar{X}$ Faeces (number)				Nests (total)			
	High	Low	t_{19}	P	High	Low	t_{19}	P	High	Low	t_{19}	P	High	Low	X^2	P
O. irroratus	42.0	15.7	3.99	<.001	8.7	7.0	0.86		26.6	27.5	0.68		18	1	15.21	<.001
R. pumilio	2.5	2.6	0.31		5.5	6.6	1.21		22.1	35.0	1.72		12	3	5.40	<.05
P. natalensis	2.7	2.4	0.47		4.4	3.5	1.09		7.4	21.7	3.01	<.01	20	0	20.00	<.001

In several instances O. irroratus and P. natalensis, but not R. pumilio, moved all or most nesting material into the chamber in which the nest was constructed. This occurred in seven O. irroratus and four P. natalensis. In addition, five O. irroratus (all of them males) moved carrots from low-cover to high-cover chambers; in these cases consumption of carrot in low-cover chambers was scored as zero. A similar phenomenon (i.e. dragging about of large food items) was recorded during observational studies (section 4.3.3).

3.3.4. Food and water deprivation

In this section body mass curves represent proportions of mean body mass recorded during five-day periods on standard laboratory diets (section 2.4.1) which preceded each trial (i.e. as g/ad libitum g body mass). In other words, data on mass loss and gain are presented as proportions of 1g of the pre-deprivation mass of each animal. This has been done to allow easy reading of figures and statistical comparison of data pertaining to animals of different mass (section 1.2.3). Similarly, food and water consumption histograms respectively represent kJ/ad libitum g body mass and ml/ad libitum g body mass.

Where responses to deprivation differed significantly between the sexes of a particular species, the sexes are treated separately; otherwise, no such distinction is made.

3.3.4.1. Responses of captive animals to food deprivation

Figure 12 illustrates changes in the proportion of body mass and water consumption in O. irroratus, R. pumilio and P. natalensis associated with periods of ad libitum food and water availability before and after

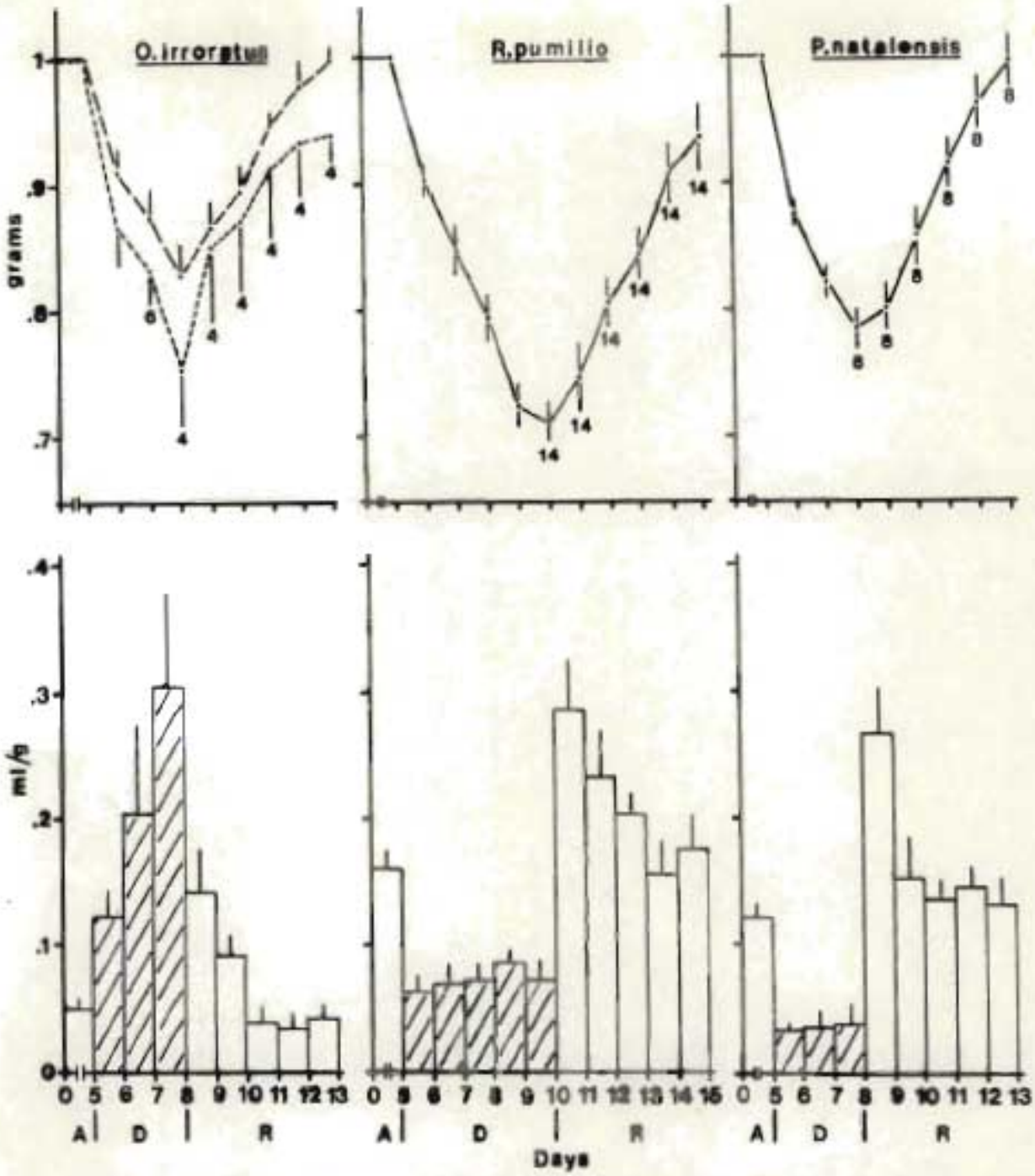

Figure 12. Effect of food deprivation on mean body mass (curves) and water consumption (histograms) of O. irroratus males (— —) and females (----), and in R. pumilio and P. natalensis. A, R = 5-day periods under conditions of ad libitum food and water availability; D = food deprived; vertical bars = 2 SEM above and/or below the mean; sample size = 16 animals of each species (8 males, 8 females), except as indicated by numbers in the body of the figure.

food deprivation, and during fasting. The most important information contained in Figure 12 may be summarized as follows:

SURVIVAL OF FOOD DEPRIVATION. All eight O. irroratus males survived three days of fasting; two females were withdrawn before reaching two days without food, while one died and one was withdrawn before reaching three days. Fourteen R. pumilio survived five days of fasting; one male and one female were withdrawn before reaching five days. Eight P. natalensis survived three days of fasting; one female died, and three females and four males were withdrawn before reaching three days.

MASS (g/ad libitum g body mass). Mean proportion of body mass of O. irroratus males and females, R. pumilio and P. natalensis after three days of fasting, and at the end of the five-day recovery period are compared statistically (Student's t) in Table 14. The most important differences were as follows: mean proportion of mass of O. irroratus males was higher than that of females at the end of both the deprivation and recovery periods; mean proportion of mass of R. pumilio (after three days of fasting) was lower than that of O. irroratus males, but higher than that of females; at the end of the deprivation period mean proportion of mass of P. natalensis was lower than that of O. irroratus males; mean proportion of mass of P. natalensis was higher than that of O. irroratus females (but not of males) after recovery; and while mean proportion of mass of R. pumilio (which had undergone five days of fasting compared with three in the other two species) was lower than that of O. irroratus males and P. natalensis, it was not significantly different from that of O. irroratus females.

WATER CONSUMPTION (ml/ad libitum g body mass). Water consumption during the initial ad libitum period was significantly higher in

Table 14. Interspecific analysis (Student's t) of mean proportion of mass (g/*ad libitum* g body mass) of captive *O. irroratus* males and females, *R. pumilio* and *P. natalensis* in relation to food deprivation (Figure 12). P given where values of t exceed the 5% level of significance.

A. Mean mass after three days of food deprivation

SPECIES + SEX / SPECIES + SEX	*O. irroratus* females	*R. pumilio*	*P. natalensis*
O. irroratus males	$t_{10} = 3.28$; $P<.01$	$t_{20} = 1.78$; $P<.05$	$t_{14} = 3.17$; $P<.01$
O. irroratus females		$t_{16} = 2.04$; $P<.05$	$t_{10} = 1.59$
R. pumilio	$t_{16} = 2.04$; $P<.05$		$t_{20} = 0.48$

B. Mean mass after five days of recovery following food deprivation.

SPECIES + SEX / SPECIES + SEX	*O. irroratus* females	*R. pumilio*	*P. natalensis*
O. irroratus males	$t_{10} = 6.87$; $P<.001$	$t_{20} = 7.82$; $P<.001$	$t_{14} = 0.36$
O. irroratus females		$t_{16} = 0.30$	$t_{10} = 8.65$; $P<.001$
R. pumilio	$t_{16} = 0.30$		$t_{20} = 8.06$; $P<.001$

R. pumilio than in P. natalensis (t_{158} = 2.04; P<.05), and significantly higher in P. natalensis than in O. irroratus (t_{158} = 9.62; P<.001). O. irroratus elevated water consumption by 156%, 323% and 535% on days one two and three of fasting respectively; by the third day of the recovery period water consumption approximated that during the initial ad libitum period. Both R. pumilio and P. natalensis depressed water consumption during food deprivation, by daily averages of 56% and 72% respectively. By the second day of the recovery period water consumption in P. natalensis was approximately normal, but in R. pumilio this did not occur until the fourth day.

Activity levels in O. irroratus, R. pumilio and P. natalensis before, during and after fasting are illustrated in Figure 13; the following summarizes the main content of this figure:

SURVIVAL OF FOOD DEPRIVATION. The period of food deprivation was limited to two days in O. irroratus and P. natalensis trials, and to three days in the R. pumilio trial. One O. irroratus female died, and one female and two males were withdrawn before reaching two days without food, but all P. natalensis survived two days of fasting (although this species performed worse than O. irroratus in the food deprivation experiment described above). One female R. pumilio died and one male was withdrawn before reaching three days, and one female died during the first day of the recovery period.

ACTIVITY (km/h). Under conditions of ad libitum food and water availability prior to fasting mean activity of O. irroratus was significantly lower than in either R. pumilio (t_{158} = 5.89; P<.001) or P. natalensis (t_{158} = 5.69; P<.001), between which there was no

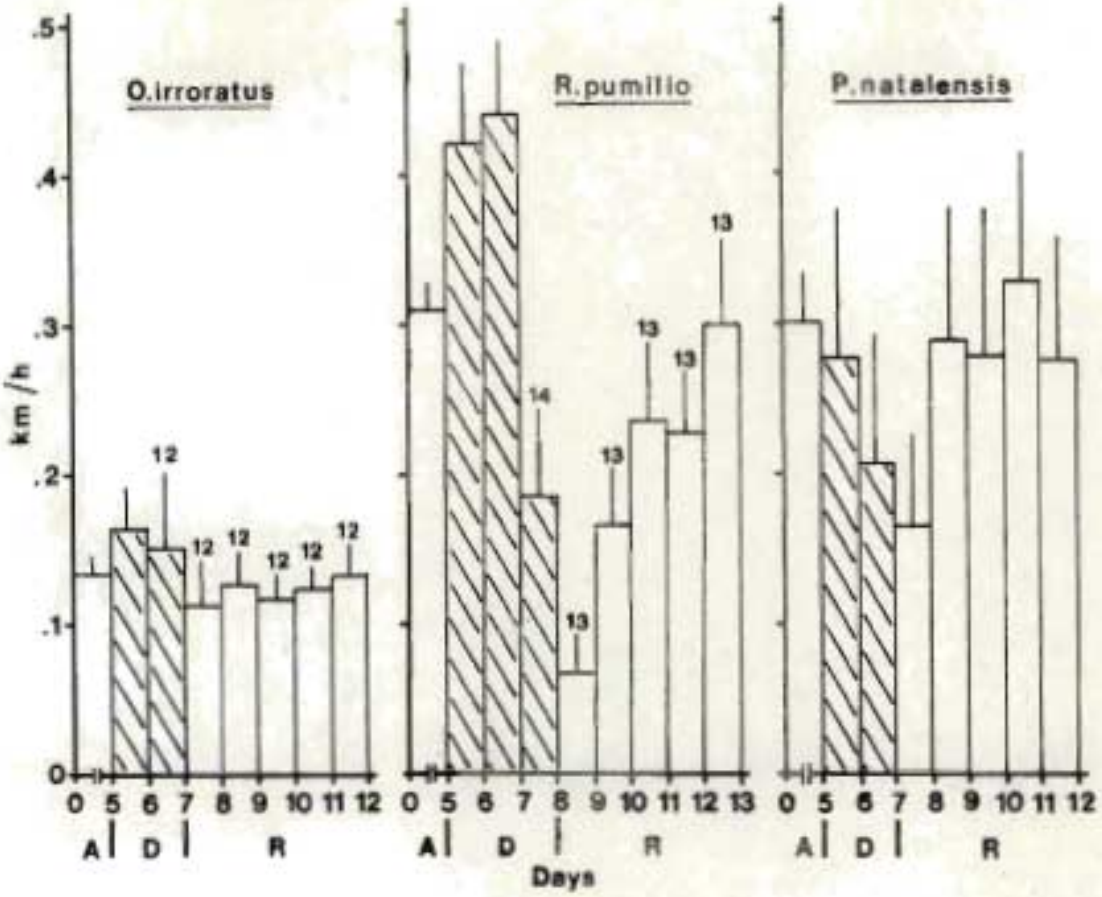

Figure 13. Effect of food deprivation on activity of O. irroratus, R. pumilio and P. natalensis. A, R = 5-day periods under conditions of ad libitum food and water availability; D = food deprived; vertical bars = 2 SEM above the mean; sample size = 16 animals of each species (8 males, 8 females), except as indicated by numbers in the body of the figure.

significant difference (t_{158} = 0.19; P>.05). O. irroratus did not significantly increase activity while food deprived (t_{106} = 0.89; P>.05), and post-deprivation activity on all five days approximated the pre-deprivation level. R. pumilio significantly increased activity during the first two days of fasting (t_{110} = 3.27; P<.001), but by the third day the animals were exhausted, and activity declined to significantly below the pre-deprivation level (t_{92} = 2.91; P<.01). Fasting P. natalensis significantly reduced activity (t_{110} = 1.93; P<.05). Return to the pre-deprivation activity level took longer in R. pumilio than P. natalensis, although had R. pumilio fasted for only two days the recovery rates of the two species would probably have been similar.

3.3.4.2. Responses of captive animals to water deprivation

Water deprivation effects on the three species (Figure 14) may be summarized as follows:

SURVIVAL OF WATER DEPRIVATION. All O. irroratus and P. natalensis survived 10 days, and all R. pumilio three days without water, but two P. natalensis (one male, one female) died on the first day of the recovery period. (It had been confidently anticipated that R. pumilio would better tolerate water deprivation than the other two species - see sections 1.2.4, 1.2.5. However, in a trial run undertaken in the animal house prior to the experiment reported here, an entire batch of eight R. pumilio was inadvertently allowed to die by subjecting them to water deprivation for four days.)

MASS (g/*ad libitum* g body mass). O. irroratus maintained mass for the full 10 days; for this reason no recovery period was warranted for

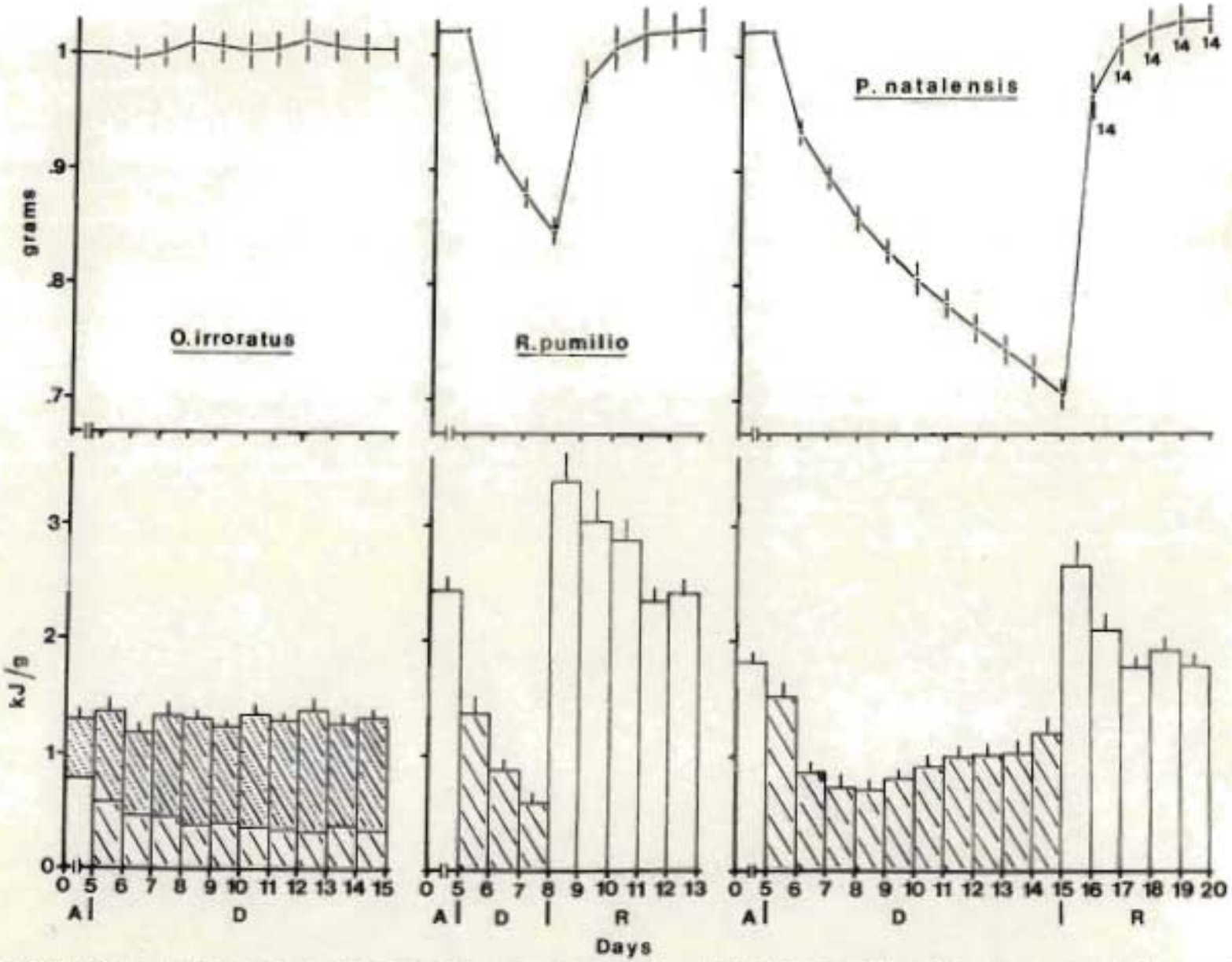

Figure 14. Effect of water deprivation on mean body mass (curves) and food consumption (histograms - dotting indicates carrot; otherwise mouse cubes) of O. irroratus, R. pumilio and P. natalensis. A, R = 5-day periods under conditions of ad libitum food and water availability; D = water deprived; vertical bars = 2 SEM above or above and below the mean; sample size = 16 animals of each species (8 males, 8 females), except as indicated by numbers in the body of the figure.

this species. Rates of loss of mass were similar in R. pumilio and P. natalensis to the third day without water when R. pumilio trials were curtailed, and mean proportion of mass of the two species was not significantly different at that time (t_{30} = 0.97; P>.05). By the end of the deprivation period mean proportion of mass of O. irroratus was significantly higher than in either R. pumilio (t_{30} = 5.02; P<.001) or P. natalensis (t_{30} = 8.94; P<.001), while that of R. pumilio was significantly higher than of P. natalensis (t_{30} = 5.79; P<.001). The rate of recovery of those P. natalensis which survived was rapid, and by the end of the first day of the recovery period there was no significant difference between mean proportion of mass of this species and of R. pumilio (t_{28} = 1.12; P>.05).

FOOD CONSUMPTION (kJ/ad libitum g body mass). Ad libitum food consumption was significantly lower in O. irroratus than in P. natalensis (t_{158} = 2.79; P<.01), and in P. natalensis than in R. pumilio (t_{158} = 3.42; P<.001), presumably at least in part reflecting the differences in sizes and associated surface-volume ratios of the three species (mean mass during pre-deprivation period: O. irroratus = 162.7g; R. pumilio = 46.8g; P. natalensis = 60.4g). Overall food consumption by O. irroratus remained approximately constant throughout the ad libitum and water deprived periods, but the proportion of carrot taken in the absence of water increased to a mean level that was significantly higher than under conditions of ad libitum water availability (t_{238} = 3.38; P<.001). This increase doubtless related to the high proportion of water contained in carrot (approximately 87% at 25°C) relative to mouse cubes (approximately 11% at 25°C). Mean volume of water present in food consumed during ad libitum water availability, calculated for consumption at 25°C, was 0.21 ml/g

ad libitum g body/mass/day (0.20ml from carrot, 0.01ml from cubes), and during water deprivation 0.37ml/g/day (0.37ml from carrot, 0.001ml from cubes). Both R. pumilio and P. natalensis significantly reduced mean food consumption during water deprivation relative to that during ad libitum water availability prior to deprivation (respectively, $t_{126} = 4.01$; $P<.001$; and $t_{238} = 3.16$; $P<.001$). There was, however, a tendency for P. natalensis to increase food consumption after the third day without water. Food consumption in both R. pumilio and P. natalensis increased on the first day of the recovery period to a level that was significantly higher than that prior to deprivation (respectively $t_{94} = 3.61$; $P<.001$; $t_{92} = 4.10$; $P<.001$). Thereafter mean food consumption declined to a level which, by the third or fourth day of the recovery period, approximated the pre-deprivation level.

The ability of P. natalensis to survive water deprivation for more than three times as long as R. pumilio (Figure 14) raises interesting questions regarding the geographical distribution (section 1.2.4) and hence ecological tolerances of the two species. Since R. pumilio occurs in the driest parts of Southern Africa, where water is an apparently limiting resource (Christian 1979a), it had been expected that even on relatively dehydrated food (i.e. mouse cubes : 10.8% and 14.4% water at 25°C and 15°C respectively) this species would display high tolerance to water deprivation. Accordingly, the ability of R. pumilio and P. natalensis to survive water deprivation under more harsh conditions (viz. 35°C, 20% RH during the light period; 15°C, 70% RH during the dark period) than those previously employed (e.g. Figure 14; 25°C, 50% RH; 15°C, 70% RH) was tested (Figure 15). Food consumption was not measured

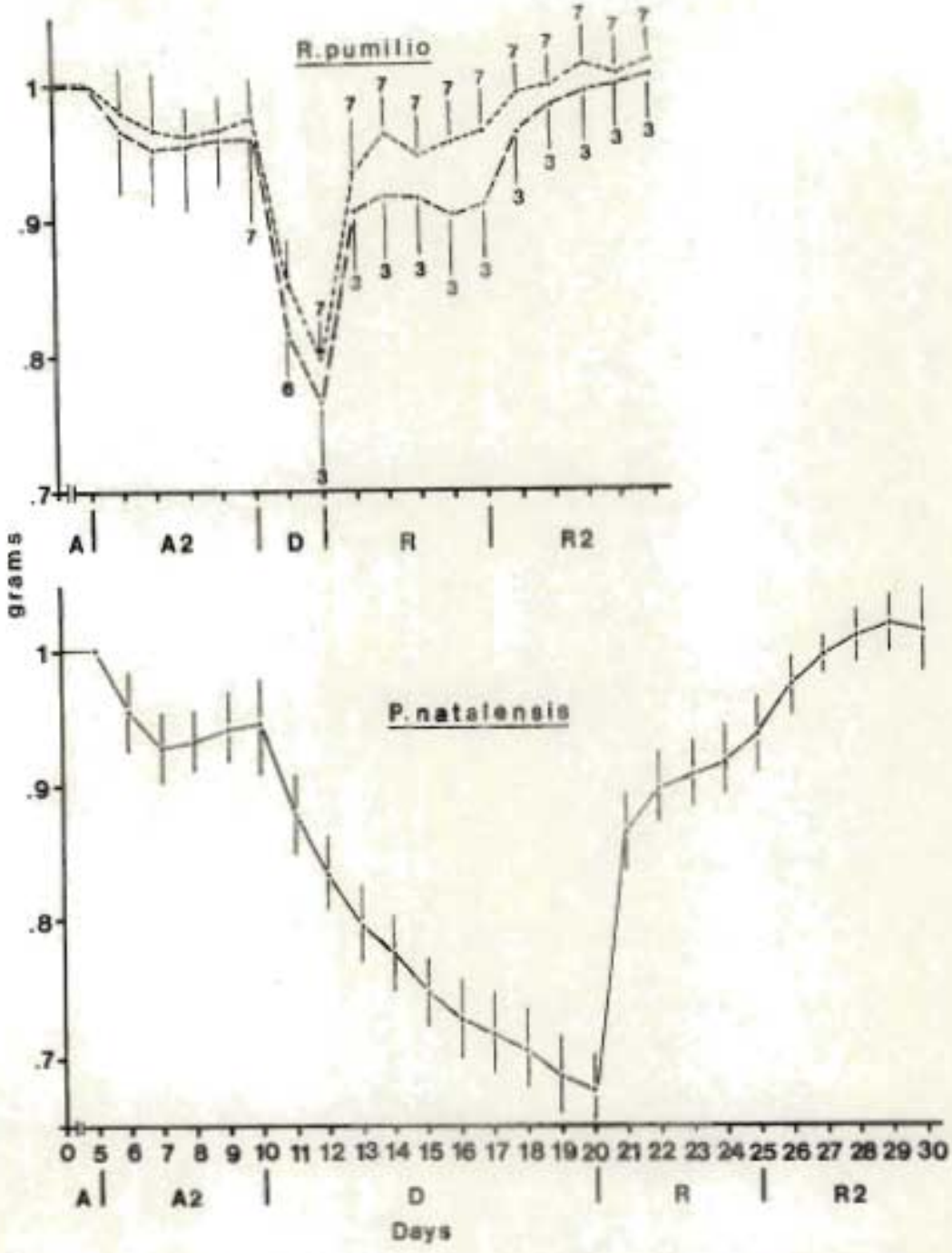

Figure 15. Effect of water deprivation under harsh environmental conditions on mean body mass of R. pumilio males (——) and females (----), and P. natalensis. A, A_2, R, R_2 = 5-day periods under conditions of ad libitum food and water availability; A, R_2 : standard environment; A_2, R : harsh environment; D = water deprived under harsh environmental conditions; vertical bars = 2 SEM above and/or below the mean; sample size = 16 animals of each species (8 males, 8 females), except as indicated by numbers in the body of the figure.

during these trials. The most important content of Figure 15 is as follows:

RESPONSE TO INCREASE IN ENVIRONMENTAL HARSHNESS. In both species mean mass declined in period A_2 relative to period A, with minimum mass reached by the second or third day (period A_2), and a tendency to increase again thereafter.

SURVIVAL OF WATER DEPRIVATION. All 16 P. natalensis survived 10 days without water, and in contrast to the earlier water deprivation experiment where two animals died during the recovery period (Figure 14), all recovered in spite of the harsher conditions. The difference in survival was not significant, however (χ^2 = 0.13; P>.05). One male R. pumilio died before commencement of deprivation, and another before the end of the first day without water, while three males and one female died before reaching the end of the second day of deprivation, when water was again provided.

MASS (g/ad libitum g body mass). From the first day under harsh environmental conditions to the end of the experiment R. pumilio females maintained a higher proportion of original body mass than did males. Comparison with mean proportion of mass at the end of the second day without water under standard environmental conditions (Figure 14) showed the R. pumilio male and female means at the termination of deprivation under harsh conditions (Figure 15) to be significantly lower (males : t_{17} = 2.98; P<.01; females : t_{21} = 2.01; P<.05). In contrast the equivalent P. natalensis means after 10 days of deprivation were not significantly different (t_{30} = 0.39; P>.05). The two species displayed similar patterns of mass recovery following deprivation, with neither returning to their original mass

until standard environmental conditions (e.g. Figure 14) had been restored.

3.4. Discussion

3.4.1. Water

The negative correlation between the distribution of O. irroratus and distance from the stream on the Dargle grassland (section 3.3.2.1) was apparently related to availability of dense cover close to water (section 3.3.3.1). The presence of water itself may be of little direct importance, however, since this species did not need to drink during water deprivation trials (section 3.3.4.2). Hence, it seems that the pattern of distribution of O. irroratus on the Dargle grassland (section 3.3.1) (as well as its reputed general preference for mesic habitats; section 1.2.5), was only secondarily related to water availability, and that vegetative cover and associated factors, themselves largely dependent on water, were more important in this respect. These factors are discussed in section 3.4.2.

The preference of O. irroratus and R. pumilio for dry chambers in which to nest (section 3.3.2.2) probably reflected their choice of nest-sites in the field, which was apparently determined by availability of plant species providing suitable cover for their domiciles (see section 3.4.2). P. natalensis did not discriminate between wet and dry chambers for nesting (section 3.3.2.2), which was surprising in view of the avoidance by this species of areas at Darvill where standing water was present (section 3.3.2.1). It is likely, however, that those animals selecting a moist environment in which to nest did so on the basis of differences in relative humidity rather than substrate moisture. RH was

measured on only one occasion (at 24°C during the final P. natalensis trial), averaging 97% in the wet chambers and 62% in the dry. In P. natalensis burrow systems RH is presumably high, and the wet chambers may have provided a nesting environment similar to that experienced by free-living animals, although their avoidance of marshy areas at Darvill (section 3.3.2.1) appears to infer an inability to burrow and nest in such areas.

Swimming was qualitatively best developed in P. natalensis which used strong undulations of the tail combined with a ventro-lateral sculling motion of the hind limbs during forward movement (section 3.3.2.3). In the two other species undulations of the tail were less powerful than in P. natalensis, and both fore- and hind-limbs were moved directly beneath the body in a motion analogous to terrestrial running. The long fur of O. irroratus and P. natalensis (section 1.2.3) which formed a "ruff" of unwetted hair round the neck (section 3.3.2.3), assisted in maintaining buoyancy in these species. R. pumilio is relatively short-haired (section 1.2.3), and lacking a "ruff" its body inclined more rapidly from the horizontal, so that attempts to propel itself forward became ineffectual more quickly than in the other two species (section 3.3.2.3).

A number of additional observations in respect of the swimming ability of the three species warrant recording, as follows:

Animals of all three species trapped during an earlier study (Willan & Meester 1978) and released into a pond approximately 2m wide, swam rapidly from the point of release to the opposite bank, and escaped into the surrounding undergrowth. On several occasions P. natalensis dived beneath the surface on release, and swam under water to the opposite bank. This behaviour was not observed in the present study,

suggesting that the test situation (section 3.2.2) was not conducive to diving.

C.N.V. Lloyd (Pers comm.), studying the direct effects of fire on survival of small mammals at Midmar Dam Nature Reserve, Natal, observed R. pumilio taking to water until the flames had passed "several minutes later", and then returning to the bank. About a week after the same fire the bodies of two O. irroratus were found in a piece of floating hydrographic research apparatus anchored midway between the banks of an inlet approximately 400m wide (A. Twinch Pers. comm.). Post-mortem showed that the animals had starved to death rather than drowned (Pers. obs.), and it seems that they had swum the 200m to the apparatus where they became trapped and subsequently died. The time of death was impossible to establish, and it is not known whether the animals entered the water to escape the fire or on account of food shortage on the burn.

Duration of swimming was approximately equal in O. irroratus females and P. natalensis, and both endured significantly longer than O. irroratus males, which in turn endured significantly longer than R. pumilio (section 3.3.2.3).

An apparently important difference between O. irroratus males and females, which was not the case in the other two species, was that male O. irroratus used in the study were significantly heavier than females (respectively, $\bar{X}$ = 186.9g and 141.6g; $t_{18} = 2.63$; $P<.01$). This difference appears to have strongly influenced swimming performance in the two sexes of O. irroratus. Similarly, Thomomys bottae, the smallest of three species of pocket gophers (Geomyidae) tested by Hickman (1977), was shown to swim

better than the larger species. It was postulated that superior swimming ability in T. bottae was an adaptation to survival and dispersal during periodic flooding of its preferred habitat. O. irroratus frequently also occupies areas subject to flooding (section 1.2.5), and in view of the present findings (section 3.3.2.3) it would be expected that females and immature animals survive flooding in greater numbers than mature males. The reproductive strategy of this species (section 5.4.2.1) appears such that removal of adult males from the population would have little effect on fertilization rates of females once breeding resumed after recolonization of a flooded area. In spite of this, Davis (1973) noted that flooding of part of his grid had the effect of interrupting breeding and reducing population density of O. irroratus in the area. (None of the above is meant to imply that sexual dimorphism in this species is in any way related to flooding; rather, the large size of males probably has a social function - see section 4.3.3.)

The poor swimming ability of R. pumilio (above) suggests that it is less well adapted to survive flooding than are the other two species. This may be compensated for, however, by the tendency of R. pumilio to move away from mesic habitats during the breeding season, which broadly coincides with the rains in the summer rainfall region (Brooks 1974). R. pumilio is thus well represented in flood-inaccessible areas during the period of maximum danger of flooding, and areas depopulated by flooding may be rapidly recolonized, as in Brooks' (1974) study.

Well developed swimming in P. natalensis (above) implies adaptation to mesic environments, with the ability to dive and swim under water suggesting that this behaviour is used to escape predators in the vicinity of water.

Flood waters may force animals to emigrate, and may thus be beneficial to species in which vagility is low (e.g. pocket gophers; Hickman 1977). This factor is probably of minor significance in relation to the species under consideration here, since socially determined dispersal appears well developed in all three (section 5.4.2), and they are in any event considerably more mobile than the fossorial species referred to by Hickman (1977). The geographical distribution of O. irroratus, R. pumilio and P. natalensis is not limited by major rivers (section 1.2.4), and involuntary crossing of such barriers probably occurs from time to time as a result of animals being swept away by floods.

3.4.2. Cover

The results presented in section 3.3.3 are in general agreement with the conclusions reached by previous authors in respect of the cover requirements of the three species (section 3.1).

Cover is obviously of direct importance to small mammals in that it provides protection from predators, but the preference of O. irroratus for dense cover, referred to in section 3.4.1, may only in part be determined by its requirements for cover itself. The role of two important factors which relate to cover and which would influence habitat preferences, namely availability of nest-sites (for surface-nesting species such as O. irroratus and R. pumilio; section 1.2.6) and food supply, are discussed below. It would perhaps be preferable to first deal with nest-site availability as being more directly a function of cover than is food supply, but here the order is reversed since the domiciles of O. irroratus are discussed jointly with those of R. pumilio.

As a specialist herbivore (section 1.2.6), the food supply of O. irroratus is probably most abundant in mesic, well vegetated habitats. As a critical limiting factor, food availability doubtless exerted a powerful influence on the distribution of O. irroratus on the Dargle grassland, where vegetation gradients, in terms of species diversity and standing crop, were extreme (Willan Unpubl.). O. irroratus has previously been recorded as utilizing a diversity of plant foods within a given study area (Davis 1973; Perrin 1980a). Of the 70 plant species recorded on the Dargle grassland (section 3.2.1.1) at least 20 (29%) provided food for O. irroratus (Willan Unpubl.); since these were utilized in the field rather than in laboratory trials where only a limited choice was available (e.g. Curtis & Perrin 1979), they may be regarded as palatable to this rodent. Only two of the plant species in question (Hyparrhenia hirta and H. quarrei, both grasses) were common in the area, so that while a wide variety of food plants was available to O. irroratus, the majority were either uncommon or rare. Although only one of the palatable species (H. quarrei) was significantly most abundant near the stream, 14 of the remaining 19 recorded food plants were either restricted to or most common in areas of high vegetative cover near to water. It is likely, therefore, that the preference of O. irroratus for such areas was at least in part determined by availability of palatable foods.

The preference of O. irroratus and R. pumilio for high-cover chambers in which to nest (section 3.3.3.2) apparently reflected their choice of nest-sites in the field. Eight O. irroratus and five R. pumilio nests were located on the Dargle grassland, and none at the other two sites (Willan Unpubl.). The nests were all situated under grasses (Aristida junciformis, Diheteropogon amplectens or Eragrostis curvula) which are perennial and form dense tussocks (Tainton et al 1976). Such grasses presumably provide

cover against rain and wind to animals nesting under them. The vegetation on the Dargle grassland had not been burned for at least three years (prior to afforestation; section 3.2.1.1), and the cover provided by these grasses was so dense that even during torrential rainfall the soil beneath them was only slightly wetted. A possible additional advantage to animals nesting under these particular grasses is that when mature all are unpalatable to livestock (Tainton et al 1976), and possibly to other large herbivores. Thus, while small mammal population densities may decline in grazed relative to ungrazed habitats (Davis 1942), surface-nesting species selecting nest-sites under unpalatable vegetation would suffer less disturbance than if palatable vegetation were selected. No O. irroratus or R. pumilio nests were located under cover provided by Themeda triandra, a highly palatable species (Tainton et al 1976), and the most common in the area. In contrast A. junciformis and D. amplectens were far less common, while E. curvula accounted for less than 2% of overall cover. This suggests, therefore, that suitable nest-sites may have been in short supply at the Dargle grassland, and possibly represented a limiting resource in respect of O. irroratus and R. pumilio.

The general activities of R. pumilio were apparently uninfluenced by cover availability within the ranges recorded in the present study (section 3.3.3.1), although this species appears to require dense cover under which to nest (above).

The preference of free-living P. natalensis for dense ground-cover at the Dargle plantation (section 3.3.3.1) may have been the result of some restriction other than cover. Two possibilities suggest themselves, namely that the spotted eagle owl Bubo africanus which was resident in the plantation (section 3.2.1.1) removed animals which ventured from cover, or

that feeding opportunities were better in the grassy verges than in the plantation itself. The presence in the plantation proper of abundant wattle Acacis mearnsii seeds, which were utilized as food by P. natalensis (Willan Unpubl.), suggests that predation may have been the more important of these two factors. Moreover, P. natalensis is generally known not to be restricted to dense vegetation (section 3.1). Nesting under high cover in the present captive study (section 3.3.3.2) doubtless reflects the habit of free-living animals of nesting in burrows (section 1.2.6). The fact that most faeces were deposited in low-cover chambers was probably related to nest sanitation (i.e. a tendency to defaecate in the open rather than in the burrow; see section 4.3.1).

3.4.3. Food and water deprivation

Fourteen out of 16 R. pumilio survived five days of fasting (section 3.3.4.1), and this species is clearly better adapted to survive periods of food shortage in the field than either of the other two. O. irroratus appeared better adapted than P. natalensis in this respect, although the difference between numbers of animals surviving three days of food deprivation in the laboratory (respectively 12 and 8) was not significant ($\chi^2 = 0.80$; $P>.05$).

It was noted by Brooks (1974) that R. pumilio carries large reserves of visible fat, and in the present study this species consistently carried more fat than either of the other two (Pers. obs.). Perrin (1981a) has shown in a quantitative study that R. pumilio contains more fat than O. irroratus. This difference was interpreted as reflecting differences in the feeding habits of the two species, with O. irroratus adapted to stable food availability, and R. pumilio exploiting more nutritious but ephemeral

foods (Perrin 1981a). In addition, the present study suggests that stored fat in R. pumilio may act as an energy reservoir permitting survival of prolonged periods of food shortage, as for example during enforced emigration of an extensive burn (below).

While a number of significant differences existed in mean proportion of mass after three days of fasting (section 3.3.4.1), these were all the result of the different tolerances of O. irroratus males and females (below). However, values for the three species were similar when data for the two sexes of O. irroratus were combined; this also applies to mass recovery after fasting. R. pumilio would doubtless have regained mass as rapidly as the other two species had it been food deprived for only three days.

The greater tolerance to food deprivation of male O. irroratus relative to females (section 3.3.4.1) suggests higher survival of males during food shortage in the field. The reason for this is not clear, but probably relates to mass differences between the sexes. Prior to food deprivation mean mass of male O. irroratus (189.7g) was significantly greater than that of females (141.2g) ($t_{14} = 2.81$; $P<.01$); this difference (34%) approximated that recorded in the field (Pers. obs.), and reflects the well developed sexual dimorphism in this species (section 1.2.3). A lower surface/mass ratio would result in reduced energy (heat) loss compared to conspecifics with a higher surface/mass ratio. Assuming similar metabolic rates and energy expenditure on activity while fasting, differential heat loss probably accounted for the observed differences in survival of the two sexes of O. irroratus. Sexual dimorphism is not well developed in R. pumilio and P. natalensis (section 1.2.3), and there were no intersexual differences in survival during food deprivation in

these species.

The patterns of activity displayed by the three species in relation to fasting (section 3.3.4.1) suggest that R. pumilio would increase and P. natalensis would decrease locomotor activity in the event of suddenly reduced food supply in the field, while O. irroratus would maintain activity levels similar to those preceding reduced availability of food. Fire is the factor most likely to cause a sudden reduction in food supply of free-living rodents in Southern Africa. In grassland and similarly combustible habitats fire may eliminate the food of O. irroratus and other Otomys spp. (Green & Taylor 1975; Swanepoel 1981; Bigalke & Willan In press), as may other causes of vegetation removal (Green & Taylor 1975). In contrast, vegetation in mesic areas (such as along water courses) is less prone to burn than is more xeric vegetation, as defined in section 3.1, a fact previously noted by Vesey-Fitzgerald (1966), and referred to by Willan & Bigalke (In press). Naturally, mesic habitats may burn from time to time, but not with the same frequency as xeric ones, where fire often occurs annually or biennially (Phillips 1965). Many Southern African animal species, including several rodents, have been shown to be fire-adapted, in the sense that they benefit from or otherwise adjust to circumstances brought about by fire (Bigalke & Willan In press). Such species may be regarded as fire-adapted, even though the adjustment made may be to emigrate from the burn.

Since the food supply of O. irroratus may be eliminated by fire (above), the failure of this species to increase its level of activity in the experiment in question (section 3.3.4.1) suggests that it would be unlikely to do so on a burn, and hence that it is poorly fire-adapted. This indicates that it is primarily adapted to mesic (less combustible)

habitats rather than to more xeric, combustible ones.

Fire probably reduces rather than eliminates the food supply of omnivorous rodents such as R. pumilio and P. natalensis (C.N.V. Lloyd Pers. comm.). The activity responses of these two species to fasting apparently reflect the ways in which they cope with food shortage after fire, R. pumilio by emigration, and P. natalensis by remaining on or near the burn (Green & Taylor 1975; Christian 1977b; Meester et al 1979; Mentis & Rowe-Rowe 1979; Swanepoel 1981; Bigalke & Willan In press). P. natalensis would be expected to reduce locomotory energy expenditure on the burn (section 3.3.4.1), thus accommodating for lower food availability. Both the R. pumilio and P. natalensis strategies outlined above may be seen as adaptations to relatively xeric, combustible habitats (section 3.1).

An additional question in respect of survival in relation to fire of R. pumilio and P. natalensis (whose food supply may not be eliminated; above) relates to the possibility of increased predation resulting from reduced vegetative cover. Differences between the patterns of diel activity and nesting habits of R. pumilio and P. natalensis (section 1.2.6) may partially account for the different ways in which they respond to fire (Bigalke & Willan In press). Being largely diurnal and generally nesting on the surface, R. pumilio would be more vulnerable on a burn to predation by diurnal raptors, which hunt by sight, than in areas of better vegetative cover. In contrast, P. natalensis nests in a burrow, which would itself afford some protection against predators, and is nocturnal, thus being vulnerable mainly to nocturnal predators such as owls. However, Christian (1977b) noted that the owls Tyto alba and Bubo africanus were absent from a burn, but hunted on a nearby unburnt control. In the absence

of evidence from areas other than that considered by Christian (i.e. a desert grassland in Namibia), it can only tentatively be suggested that levels of nocturnal predation, at least by owls, may in general be lower in burnt than in unburnt habitats.

Water consumption under conditions of ad libitum food availability was lowest in O. irroratus (section 3.3.4.1), presumably reflecting the fact that part of its diet (carrot) contained approximately eight times as much preformed water as did mouse cubes (section 3.3.4.2), on which the other two species were fed. The water requirements of free-living O. irroratus probably change with seasonal variation in levels of hydration of the plant material on which it feeds.

The significant difference in ad libitum water consumption of R. pumilio and P. natalensis (section 3.3.4.1) may at least in part have been related to differences in levels of hydration of their food (mouse cubes) during the day and night parts of the light cycle (section 3.2.2). Mouse cubes contained 10.8% water during the light period when R. pumilio was most active, and 14.4% during the dark when P. natalensis was active (Pers. obs.). These activity patterns were similar to those of free-living animals (section 1.2.6). Assuming the water content of dry seeds to vary according to temperature and relative humidity in the field, R. pumilio would appear to obtain less water than P. natalensis from this food source. However, R. pumilio probably consumes greater quantities of highly hydrated foods than P. natalensis, namely invertebrates (Willan Unpubl.) and green plant material (Kingdon 1974), although Perrin (1980a) has shown that at least in the Eastern Cape R. pumilio is not primarily a herbivore, as reported by Kingdon (1974). It is thus probable that free-living R. pumilio require less drinking water than P. natalensis, not more as in

the captive study (section 3.3.4.1).

In terms of Wright's (1976) hypothesis, water consumption during food deprivation had been expected to decline in O. irroratus, and to rise in R. pumilio and P. natalensis (section 3.1). The fact that while fasting both R. pumilio and P. natalensis depressed drinking (section 3.3.4.1) suggests that these species are primarily mesophilous (Wright 1976), and the occurrence of R. pumilio in the S.W. Arid is probably explained by its ability to efficiently utilize invertebrate food (below). Taking into account the large amount of preformed water obtained from its food by O. irroratus (0.21ml/g body mass/day; section 3.3.4.2), this species depressed drinking while fasting by a daily average of 18% of total (preformed plus free) ad libitum water consumption. O. irroratus may thus also be classified as mesophilous (Wright 1976), which is in keeping with other information on the habitat preferences of this species (section 1.2.5). The amount of water obtained from mouse cubes by R. pumilio and P. natalensis (approximately 0.02ml/g animal mass/day) was negligible relative to the large amounts obtained from carrot by O. irroratus. The small decline in total water consumption of fasting O. irroratus was to be expected in view of the highly hydrated nature of its food.

The high tolerance of O. irroratus to water deprivation (10 days without mass loss on a diet which included carrot) was expected in view of the high proportion of water in its food (section 3.3.4.2). In contrast, the patterns of geographic distribution of R. pumilio and P. natalensis (section 1.2.4) had suggested that their responses would be the reverse (relative to one another) of those observed (i.e. that R. pumilio would perform better than P. natalensis). It is probable that the difference in the ability of R. pumilio and P. natalensis to survive without water (respectively three and 10 days) is at least in part

explained by differences in the amount of free water available to the two species in their food (see above). In addition, evaporative water loss in P. natalensis was probably lower than in R. pumilio, the difference being explained by differences in the ambient temperatures and relative humidities at which the two species were active (section 3.2.2). The magnitude of the difference in survival strongly implies that free-living P. natalensis are physiologically better equipped than R. pumilio to tolerate water shortage (see discussion of factors apparently influencing the geographic distribution of these two species, below).

The conclusion that P. natalensis is probably physiologically better adapted to water stress than is R. pumilio (above) was reinforced by the observed responses of the two species to water deprivation under harsh environmental conditions (section 3.3.4.2). P. natalensis elevated water consumption by less than one-tenth of the average increase exhibited by R. pumilio when environmental conditions were made more extreme, and while all P. natalensis survived 10 days without water, the R. pumilio trials had to be terminated after two days to avoid further mortality after six had died. P. natalensis performed more or less equally well under standard and harsh conditions, presumably because the environments in the two sets of trials were the same during the dark period when this species was active. R. pumilio performed significantly less well under harsh conditions than under standard, apparently reflecting the influence of increased temperature, and of reduced relative humidity and water content of mouse cubes (7%) during the light period, when most activity occurred.

Male R. pumilio were less tolerant of harsh environmental conditions than were females (section 3.3.4.2). This was not anticipated since males used in the experiment were larger ($\bar{X}$ = 53.7g), and thus would have been

expected to better withstand the effects of dehydration than females ($\bar{X}$ = 46.8g). The explanation may partly lie in differences in behavioural responses to deprivation of the two sexes. Activity in relation to water deprivation was not quantitatively measured, but in all deprivation experiments (sections 3.3.4.1, 3.3.4.2) male R. pumilio tended to be more active and spent more time attempting to escape from their cages than did females. In activity/fasting trials (section 3.3.4.1) the difference was not significant (t_{44} = 0.97; P>.05), but male activity was 7% higher than in females. The difference was probably of similar magnitude during other deprivation trials, and while this was apparently not critical during water deprivation under standard conditions it probably contributed to the lower survival of males under harsh conditions when evaporative water loss was high. Coupled with this, captive R. pumilio males tended to accumulate more visible fat than did females, and this may have contributed to their low survival rate under harsh conditions. While oxidization of fat provides more water (g) than the mass of fat metabolized, increased oxygen requirements may result in respiratory water loss in excess of oxidative gain (Schmidt-Nielsen 1965), and such loss increases with increasing temperature (Ingram & Mount 1975). Hence, while it was postulated (above) that fat storage in R. pumilio may be an adaptation to prolonged survival without food, survival without water appears not to benefit from this factor, at least for R. pumilio studied under harsh environmental conditions as defined in this study.

(Perrin 1981b observed that free-living R. pumilio females are fatter than males. Fat accumulation in captive males of this species was probably the result of lower activity levels than in the field, where energy expenditure in reproductive activity is probably considerable; section 5.4.2.2.)

The occurrence of R. pumilio in the S.W. Arid zone (section 1.2.4) where water availability limits reproductive ability and population density (Christian 1979a), may in part be explained by the ability of this species to efficiently utilize insect food (e.g. to gain significant mass during a three-day period on a diet comprising only flying ants - Macrotermes sp. primary reproductives; Willan Unpubl.). In the S.W. Arid R. pumilio is probably largely dependent for food on seeds, which are abundant and thus more readily available than insects (Maclean 1974). However, apart from their nutritional importance to R. pumilio (Perrin 1980a) insects would be expected to provide much of the water required by this species, especially in areas of transient availability of surface water and highly hydrated plant material. An ability to cope in this way with arid-zone water shortage is known in many animal species, including birds (Maclean 1974) and small mammals (e.g. Schmidt-Nielsen 1965). Arid-zone R. pumilio probably represent a race which differs physiologically from that occurring in wetter parts of its geographic range (D.P. Christian In litt.). Furthermore, arid-zone R. pumilio probably have lower water requirements than shown by Natal midlands stock (section 3.3.4.2), and possibly a lower intake of insects than in wetter areas such as the Transvaal highveld (Brooks 1974) and Eastern Cape (Perrin 1980a).

The high tolerance to water deprivation exhibited by P. natalensis (section 3.3.4.2) was not expected in view of its preclusion from the drier parts of Southern Africa (section 1.2.4). However, this species lost significant mass on a flying ant diet (Willan Unpubl.). The inability of this otherwise broad-niche species (Meester et al 1979) to penetrate the S.W. Arid may thus result from its apparently poor utilization of insect food.

3.4.4. Conclusions

3.4.4.1. Niche separation as determined by water

A summary of the differences between the responses of the three species to the parameters investigated (section 3.3) is provided in Table 15, which includes qualifications made of these results in sections 3.4.1 - 3.4.3. Efficiency of utilization of invertebrate food by R. pumilio and P. natalensis is included in this table for the reasons set out in section 3.4.3.

In an attempt to quantify as far as possible the ecological preferences and responses in relation to water of O. irroratus, R. pumilio and P. natalensis, scores were allocated in respect of each parameter which distinguish the level of mesic or xeric adaptation of each species relative to the other two. Weighting was not employed, and although consideration was given to manipulating data in order to emphasize the apparently greater importance of some parameters than of others, this has been avoided because, in the present state of knowledge of the ecology of the three species, decisions as to relative importance would of necessity have been subjective, and hence possibly misleading. However, in several instances scores were allocated on the balance of probability rather than on purely empirical evidence, but a brief explanation of every score is provided, together with references to the text (Table 15). Scores were allocated as follows:

1 : indicating a mesophilous tendency

0 : indicating neither a mesophilous nor a xerophilous tendency

-1 : indicating a xerophilous tendency

Table 15. Summary of ecological differences between O. irroratus, R. pumilio and P. natalensis in relation to water, and quantitative comparison in terms of the parameters listed. Scores indicate the following: 1: mesophilous tendency; 0: neither mesophilous nor xerophilous tendency; -1: xerophilous tendency.

PARAMETERS	REFERENCE (section)	O. irroratus		R. pumilio		P. natalensis	
		Explanation	Score	Explanation	Score	Explanation	Score
WATER	3.3.2						
Distance from stream (Dargle grassland)	3.3.2.1	Negative correlation (apparently related to cover; section 3.4.1)	1	No correlation	0	Not present	-
Standing water (Darvill)	3.3.2.1	No correlation	0	No correlation	0	Negative correlation (but probably determined by burrowing opportunities; section 3.4.1)	0
Substrate moisture (Laboratory)	3.3.2.2	Dry nest sites	0	Dry nest sites	0	Moist nest sites (but probably determined by humidity; section 3.4.1)	0
Swimming ability (Laboratory)	3.3.2.3	Males worse than, and females similar to P. natalensis	0	Worst developed	-1	Better than O. irroratus males, and similar to females.	1

Continued overleaf

Table 15. Continued.

PARAMETERS	REFERENCE (section)	*O. irroratus*		*R. pumilio*		*P. natalensis*	
		Explanation	Score	Explanation	Score	Explanation	Score
COVER	3.3.3						
Association with cover (Dargle grassland)	3.3.3.1	Positive correlation (apparently related to feeding opportunities; section 3.4.2)	1	No correlation	0	Not present	-
Colonization of firebreak (Dargle grassland)	3.3.3.1	Later than *R. pumilio*	1	Sooner than *O. irroratus*	-1	Not present	-
Association with ground cover (Dargle plantation)	3.3.3.1	Inadequate data	-	Inadequate data	-	Positive correlation (but probably determined by predation; section 3.4.2)	0
Food consumption (Laboratory)	3.3.3.2	More under cover	1	No discrimination	0	No discrimination	0
Faeces deposition (Laboratory)	3.3.3.2	No discrimination	0	No discrimination	0	Less under cover (but probably determined by sanitation; section 3.4.2)	0

Continued overleaf

Table 15. Continued.

PARAMETERS	REFERENCE (section)	*O. irroratus*		*R. pumilio*		*P. natalensis*	
		Explanation	Score	Explanation	Score	Explanation	Score
DEPRIVATION (Laboratory)	3.3.4						
Survival of food deprivation	3.3.4.1	Better than *P. natalensis*	0	Best (five days)	-1	Worse than *O. irroratus*	1
Mass loss during food deprivation	3.3.4.1	Similar to other two species (section 3.4.3)	0	Similar to other two species (section 3.4.3)	0	Similar to other two species (section 3.4.3)	0
Mass recovery after food deprivation	3.3.4.1	Similar to other two species (section 3.4.3)	0	Similar to other two species (section 3.4.3)	0	Similar to other two species (section 3.4.3)	0
Water consumption (*ad libitum* food)	3.3.4.1	Results biased by high water content of food (section 3.4.3)	-	Probably lower than *P. natalensis* in the field (section 3.4.3)	-1	Probably higher than *R. pumilio* in the field (section 3.4.3)	1
Water consumption (food deprived)	3.3.4.1	Depressed, taking into account preformed water obtained from food (section 3.4.3)	1	Depressed	1	Depressed	1
Activity during food deprivation	3.3.4.1	Similar to normal level (suggests lack of adaptation to food shortage; section 3.4.3)	1	Increased (suggests migration during food shortage; section 3.4.3)	-1	Decreased (suggests reduced activity during food shortage; section 3.4.3)	-1
Survival of water deprivation	3.3.4.2	Results biased by high water content of food (section 3.4.3)	-	Worse than *P. natalensis*	1	Better than *R. pumilio*	-1

Continued overleaf

Table 15. Continued.

PARAMETERS	REFERENCE (section)	*O. irroratus*		*R. pumilio*		*P. natalensis*	
		Explanation	Score	Explanation	Score	Explanation	Score
DEPRIVATION (Continued) (Laboratory)							
Mass loss during water deprivation	3.3.4.2	Results biased by high water content of food (section 3.4.3)	-	Similar to *P. natalensis*	0	Similar to *R. pumilio*	0
Mass recovery after water deprivation	3.3.4.2	Not tested	-	Less rapid than *P. natalensis*	1	More rapid than *R. pumilio*	-1
Food consumption (water deprived)	3.3.4.2	Results biased by high water content of food (section 3.4.3)	-	Greater depression than *P. natalensis*	1	Lower depression than *R. pumilio*	-1
Responses to harsh environment	3.3.4.2	Not tested	-	Worse performance than *P. natalensis*	1	Better performance than *R. pumilio*	-1
ADDITIONAL FACTORS	3.4.3						
Utilization of invertebrate food	3.4.3	Does not utilize invertebrate food (section 1.2.6)	-	Better utilization than *P. natalensis*	-1	Worse utilization than than *R. pumilio*	1
TOTAL SCORE			6		-1		0
MAXIMUM POSSIBLE POSITIVE SCORE			13		20		18
INDEX OF MESIC ADAPTATION			+.46		-.05		0

Scores for each species were totalled and then divided by the maximum possible positive score, thus providing indices of mesic adaptation which represent the position of each species on a mesic/xeric continuum, arbitrarily defined as having a numerical range of 1 (100% mesophilous) to -1 (100% xerophilous) (Table 15). Clearly, ecological niches cannot be designated by isolated points on a continuum, since this takes no account of niche breadth or of intraspecific variation or individual adaptability. The indices ascribed to the three species are thus taken to represent mean values (for Natal midlands populations), around which there are at present unknown ranges of ecological tolerance which permit occupation of marginal habitats.

Distribution of the scores allocated to the three species (Table 15) was not significantly different ($H_2 = 4.23$; $P>.05$), although the O. irroratus and R. pumilio scores did differ significantly ($U = 81.5$; $P<.05$). There were no significant differences in the other possible comparisons (i.e. O. irroratus vs. P. natalensis: $U = 78.0$; $P>.05$; R. pumilio vs. P. natalensis : $U = 173.5$; $P>.05$). This analysis permits the following conclusions in terms of the parameters measured (Table 15):

O. irroratus is apparently more nearly mesophilous than either R. pumilio or P. natalensis, both of which displayed adaptations which placed them approximately midway on the mesic/xeric continuum described above. This similarity was not expected (section 3.1), and implies support for D.P. Christian's (In litt.) suggestion that savanna and arid-zone R. pumilio represent different physiological races (section 3.4.3). However, the importance of efficient utilization of invertebrate food by R. pumilio (where only -1 was scored) was probably underestimated relative to the tolerance of P. natalensis to

water deprivation (where a total of -4 was scored). Manipulations of data to compensate for this probable discrepancy would be out of place on the basis of information at present available. In any event, Perrin's (1981b) description of R. pumilio as having a xeric tendency and P. natalensis only a xeric tolerance, with O. irroratus mesically adapted, appears to have been supported without weighting of scores.

3.4.4.2. Preferred habitats and habitat stability

As pointed out in section 3.1, it is difficult to distinguish between the habitat preferences of species such as O. irroratus, R. pumilio and P. natalensis, since they are so frequently sympatric (section 1.2.5). This difficulty is added to by the wide environmental tolerances of the three species (section 1.2.5), especially when their entire geographic ranges are considered (section 1.2.4). However, it is apparent from the conclusions reached in section 3.4.4.1 that at least in the Natal midlands the habitat preferences of O. irroratus, R. pumilio and P. natalensis differ in terms of the quantity of water present in the environment.

As a major factor limiting primary productivity and length of the growing season in Southern Africa (section 3.1) water, in determining habitat preferences, presumably mainly acts indirectly by influencing plant growth in space and time. This in turn would affect the abundance and stability of the food supply of animals feeding at all trophic levels. Furthermore, other critical resources such as drinking water, nest-sites (mainly for surface-nesters such as O. irroratus and R. pumilio, but also apparently for the burrowing P. natalensis; section 3.4.4.1), and even availability of potential mates, which would themselves be adapted to select

a particular type of habitat (Krebs 1978), would be influenced by water. Thus, in general, high and constant water supply would result in high and stable resource availability. Happold (1973) reached similar conclusions in respect of resource availability in the habitats occupied by several species of conilurine rodents in Australia.

Taking into account the above general statement relating availability of resources to water supply, it is possible to make certain assumptions regarding the preferred habitats of the three species.

The mesic habitats favoured by O. irroratus would have higher and more stable resource availability than the more xeric areas preferred by R. pumilio. Perrin (1980a) has previously shown that even in the Fish River valley where rainfall is lower ($\bar{X}$ = 507mm p.a.) than in the Natal midlands (section 3.2.1.1) and may be as low as 222mm p.a., the food supply of O. irroratus is more abundant and stable than that of R. pumilio. A second important factor relating to the preferred environments of these two species is that, at least in the general area where the present study was undertaken, the grassland habitats favoured by R. pumilio are extensive, while the mesic ones favoured by O. irroratus are frequently no more than a few hectares in size.

Perrin's (1980b) paper on the breeding strategies of O. irroratus and R. pumilio includes a table of templet characteristics (i.e. ecological characteristics; Southwood 1977), in which the patch size (i.e. areas of favourable habitat; Southwood 1977) of the two species are described as follows: O. irroratus - large permanent grasslands, and R. pumilio - small areas with temporary aggregations of insects or seeds. These conclusions do not agree with my own (above).

In the Natal midlands O. irroratus does occur in grassland and is not confined to mesic habitats, but at the Dargle grassland study area this species was most abundant in lush vegetation associated with a perennial water supply (section 3.3.2.1). This type of distribution has been confirmed by observation and trapping at numerous sites in Natal and elsewhere (Pers. obs.), as well as in S.W. Cape montane fynbos (Willan & Bigalke In press) and the Transvaal highveld (Davis 1973). The implication is that the study area selected by Perrin (1980a, b, c, 1981b) may have been marginal for O. irroratus, and that the attributes of the Fish River valley population described by this author may not be representative of the species in Southern Africa.

The description of the patch size of R. pumilio as small (above) is probably not generally applicable, inasmuch as the term implies a smaller range of local movement in this species than in O. irroratus. There is no published information which would allow direct comparison of spatial patterns of habitat utilization in R. pumilio with those of O. irroratus, and data obtained in the present study were unsuitable for this type of analysis. However, information obtained in S.W. Cape montane fynbos during a single four-day CMR trapping session (December 1979) on a 100-station grid with 15m between stations (Willan Unpubl.), and using techniques which were equally suitable for both species (Willan In prep.) suggests that the movements of O. irroratus tend to be more restricted than those of R. pumilio. Calculations were made of Av.D (i.e. the mean average distance between successive captures of individual animals; Brant 1962) for the 18 O. irroratus and six R. pumilio trapped more than once (out of 30 adult O. irroratus and 23 adult R. pumilio known to be on the grid), thus providing data suitable for inclusion in the calculations (Brant 1962). Av.D for R. pumilio (nine suitable captures) was 27.5m and for O. irroratus (28 suitable captures) 15.5m. This difference is significant

(t_{35} = 2.87; P<.01), and although the sample was small, shows that at least in the habitat and at the time in question the movements of R. pumilio were almost twice as extensive as those of O. irroratus. In addition, six O. irroratus but no R. pumilio were captured more than once at the same stations. This suggests that while O. irroratus was able to find sufficient food in a restricted area, aggregations of food for R. pumilio (Perrin 1980b) did not exist.

The danger of extrapolating from the above conclusions to Natal midlands habitats and populations is fully appreciated. However, fynbos is known for its high floristic diversity (Acocks 1953), and local aggregations of food (e.g. Protea seeds) suitable for omnivorous rodents such as R. pumilio (above) would be more likely to occur in this type of vegetation than in areas such as the Natal midlands where floristic diversity is lower (section 3.2.1.1), with food (e.g. grass seeds) more continuously distributed through the habitat. Hence, it is probably safe to conclude that at least in the Natal midlands, food and other resources essential to survival and reproduction are more widely dispersed in the case of R. pumilio than in O. irroratus.

If judged only on the basis of the influence of water supply and its correlates, P. natalensis would be expected to have lesser quantities of essential resources available to it than O. irroratus and greater quantities than R. pumilio. However, P. natalensis, in addition to its habitat preferences as determined by water, is adapted to disturbed (i.e. disrupted, degraded) environments (De Wit 1972; Kingdon 1974; Meester et al 1979). In the present study this species occurred in two disturbed habitats (Dargle plantation and Darvill) but not in the relatively undisturbed Dargle grassland area or elsewhere in the vicinity (section 3.2.1.1).

Three important features of disturbed habitats may be seen as influencing the availability of resources in respect of the pioneer P. natalensis. First, disturbed habitats appear to provide this species with abundant resources, as indicated by increases in population density after fire (section 3.1), by the higher densities recorded in weed-dominated than in climax vegetation (De Wit 1972), by the higher densities in cultivated than in undisturbed areas (Coetzee 1975), and by its tendency toward commensalism (section 1.2.5). Second, as succession proceeds from a disturbed toward a climax situation, P. natalensis is replaced by more specialized rodents such as O. irroratus and R. pumilio (Meester et al 1979). Hence, the preferred habitats of P. natalensis appear markedly ephemeral in the medium or long term (see section 3.1), thus differing from those of R. pumilio which are seasonally ephemeral (Perrin 1980a). Third, while extensive areas of habitat in Southern Africa may be regarded as disturbed at present, this has clearly not always been the case. In this respect Meester et al (1979) have suggested that P. natalensis will become increasingly abundant as a result of increasing human disturbance of the environment. In the evolutionary history of this species, preferred (disturbed) habitats were no doubt less common in space and time than at present, resulting from natural perturbations of the environment and the limited activities of pre-historic man.

In summary, the following generalizations may be made in respect of the preferred habitats of the three species, at least in the Natal midlands:

O. irroratus. Mesic areas with good vegetative cover; resource availability is variable in space (i.e. small areas of optimum habitat), but within these areas is high and stable in time.

R. pumilio. Drier areas with less dense vegetation, and with resource availability less variable in space (i.e. large areas of optimum habitat), but less stable in time (i.e. seasonally ephemeral) than in the mesic habitats favoured by O. irroratus.

P. natalensis. Disturbed habitats; availability of such habitats, and hence of resources, is highly variable in space (i.e. resulting from possibly localized chance disturbance of the environment) and time (i.e. dependent on the rate of ecological succession).

4. SOCIAL BEHAVIOUR

4.1. Introduction

Social behaviour may be regarded as behaviour to do with more than one individual (Tinbergen 1953; Davis 1972; Happold 1973, 1976), behaviour which influences or potentially influences another animal (Thompson 1968), behaviour which functions principally to influence a conspecific (Ewer 1968), or, in addition, is influenced by a conspecific (Barnett 1963), and behaviour related to the natural group (Crook 1970) and group cohesion (Barnett 1963).

In this work I regard social behaviour as subordinate to social organization and ultimately to socio-ecological niche. Consequently, it is treated at the level of functional units (Huxley 1966; Eisenberg 1967) rather than discrete elements (Eisenberg 1967; Eibl-Eibesfeldt 1975), and movements are not described except where they appear to bear directly on social function or where description elucidates important interspecific differences. Sociograms (Wilson 1975) are species-specific and the units constituting them are analogous rather than homologous (Eisenberg 1967; Happold 1973, 1976). However, it is convenient to refer the social repertoires of the three species to a standardized nomenclature, as far as possible after that of Eisenberg (1967). Similarly, functional units are placed in logical order, although behavioural sequences in rodents are flexible, and much individual variation exists.

The behavioural study was undertaken to provide a standardized account of the social inventories of the three species, which would serve as a basis for analysis of their social systems. Analysis of social organization

was not possible from the available information on O. irroratus (Davis 1972, 1973), R. pumilio (Choate 1972; Brooks 1974; Marais 1974; Johnson 1980) and P. natalensis (Veenstra 1958; Choate 1972; Cilliers 1972; Coetzee 1975), since a variety of observational and descriptive methods were employed. However, behavioural development from birth to sexual maturity, and parent/young relations, have been adequately described in terms of the Williams & Scott (1953) definitions: O. irroratus (Davis 1972, 1973), R. pumilio (Meester & Hallett 1970; Choate 1971; Brooks 1974) and P. natalensis (Meester 1960; Meester & Hallett 1970; Baker & Meester 1977). In view of this coverage, and because sociograms largely refer to adult behaviour (Eisenberg 1962, 1967; Happold 1973, 1976), the animals used were all of adult weight, although half of them were not in reproductive condition.

4.2. Methods

Caging and maintenance are described in section 2.4.1, and the observation room and cages in section 2.4.2. Social behaviour of 4-6 dyads of each of 10 combinations of sexually mature and immature animals of both sexes (section 2.2) was studied on a more or less ad libitum basis (section 2.3.2) for a total of approximately 400h/species. Records were kept of behavioural postures and sequences, and of potentially social acts, namely sound production within the range of human hearing, and marking behaviour. No histological or biochemical techniques were employed to ascertain the communicatory significance of movements apparently representing marking behaviour.

Five broad categories of social behaviour were distinguished and defined as follows:

COMMUNICATION. Rendering of information and perception of the social environment; including potential stimuli such as scent marks and incidental activity sounds made in a non-social context (Happold 1973, 1976).

INITIAL CONTACT BEHAVIOUR. Investigatory; generally lacking overtly attracting or repelling elements.

AGONISTIC BEHAVIOUR. Repelling; comprising aggressive or defensive elements; tending to keep animals apart (Happold 1973, 1976).

AMICABLE BEHAVIOUR. Attracting; promotion of social contact; tending to keep animals together (Happold 1973, 1976).

SEXUAL BEHAVIOUR. Courtship and mating.

When difficulty was experienced in separating behaviour patterns, they were classified according to apparent intent and to the result of contact when established (Delgado 1966). To eliminate considerations of social hierarchy (which is dealt with in section 5) from behavioural descriptions, the terms "aggressive" ("aggressor") and "non-aggressive ("non-aggressor") are used in preference to "dominant" and "subordinate" (Happold 1973, 1976).

4.3. Results

4.3.1. Communication

Responses to activity sounds in all three species were more evident in non-aggressive than aggressive animals, the tendency being to freeze or flee. R. pumilio most frequently resorted to flight in these circumstances,

and P. natalensis least frequently.

The units of auditory communication which occurred during social interaction are listed in Table 16, together with the circumstances in which they were usually produced, and the responses they elicited. O. irroratus was consistently most vocal, and the sounds it produces are sufficiently loud to be heard at considerable distances in the field (Davis 1973). Tail-quivering occurred as part of the agonistic repertoires of all three species (section 4.3.3) but only in O. irroratus was contact between the tail and the substrate so violent as to be audible. Tail-quivering is known to provide auditory as well as visual cues in some rodents (Clark & Schein 1966; Ewer 1968), and may be well developed in species which rarely engage in biting attack (Ewer 1968). Species in which tooth-chattering occurs, such as R. pumilio, may be more prone to bite conspecifics (Ewer 1968). Sounds produced by P. natalensis are mostly in the ultrasonic (i.e. >10kHz) range (D.H. Gordon Pers. comm.), and ultrasounds have been detected in R. pumilio in association with three categories of agonistic behaviour (analogous to aggressive approach, flight and submission, as defined in this study; section 4.3.3) but were not associated with courtship and mating in this species (Johnson 1980). Sound production in O. irroratus may be concentrated at lower frequencies, judging by the apparent social significance (Table 16) of vocalizations audible to humans (i.e. <10kHz).

Movements which were interpreted as marking behaviour were infrequently observed (Table 17), and intruders showed no more interest in sites where scent marks had apparently been deposited than, for example, in places where another animal had rested. However, it is likely that in spite of regular washing of cages and replacement of furnishings, residual odour of previous inhabitants was present, thus moderating the communicatory value

Table 16. Auditory communication in *O. irroratus*, *R. pumilio* and *P. natalensis*.

SPECIES	FUNCTIONAL UNITS	DETAILS OF OCCURRENCE	TYPICAL RESPONSE
OTOMYS	LOUD "CHIT" (Davis 1973)	Extensively used by both animals in agonistic situations, increasing in frequency and intensity with decreasing distance between them; normally accompanied by an upright posture.	"Chitting" by a non-aggressor normally checked advance or caused withdrawal of an aggressor.
	ALARM SQUEAL (Davis 1973)	Issued by a non-aggressor under threat of attack by an aggressor.	Almost invariably prevented attack by an aggressor.
	TAIL-QUIVER	Used by a highly aggressive animal in an agonistic situation.	Variable (see section 4.3.3).
RHABDOMYS	SQUEAK	Rarely emitted by a non-aggressor during flight from an aggressor; Marais (1974) notes that males squeak while pursuing oestrus females.	Unknown.
	TOOTH-CHATTER	Rarely used by a non-aggressor during defensive threat (section 4.3.3).	Unknown.
PRAOMYS	MUTED SQUEAK	Occasionally emitted by a non-aggressor in an agonistic situation, usually prior to flight or submission (section 4.3.3).	Unknown.
	MUTED "CHEEP"	Produced by a non-receptive female during male sexual advances.	Unknown.

Table 17. Olfactory communication in O. irroratus, R. pumilio and P. natalensis.

SPECIES	FUNCTIONAL UNITS	DETAILS OF OCCURRENCE
OTOMYS	CHEEK-RUB	Rarely observed rubbing of the side of the face against a prominent object (e.g. a feeding dish).
	NASO-ANAL CONTACT	Relatively rare.
	PERINEAL DRAG	Common in aggressive animals, normally in an upright posture; a rare quadrupedal variation was performed by males which rapidly raised and lowered the posterior part of the body several times, forcibly applying the scrotum to the substrate.
RHABDOMYS	CHIN-RUB	Occasionally observed chinning (Ewer 1968) of small objects such as pebbles.
	NASO-ANAL CONTACT	Relatively rare.
	PERINEAL DRAG	Common in aggressive animals, particularly males, in an upright or semi-upright posture; previously identified in aggressive R. pumilio (Marais 1974), and in sexually aroused males (Choate 1972; Brooks 1974).
PRAOMYS	CHIN-RUB CHEEK-RUB NECK-RUB	Movements which occurred with greater frequency than their analogues in O. irroratus and R. pumilio, but still relatively uncommon; prominent objects such as feeding dishes and branches were marked.
	NASO-ANAL CONTACT	Relatively common in intra- and intersexual dyads, with mutual sniffing of the ano-genital region.
	GENITAL PRESENTATION	Observed in male/female dyads, with either animal turning to present the posterior to be sniffed; this was a typical unit of the P. natalensis sexual repertoire (section 4.3.5).
	PERINEAL DRAG	Common in aggressors, usually in an upright posture.

of more recent marks. In addition to the movements listed in Table 17, Davis (1972) described O. irroratus as rubbing the base of the tail against the cage wall, and suggested that the movement had a marking function, but this was not observed in the present study. In all three species, aggressive animals in agonistic situations consistently applied the perineal region, or in males the enlarged scrotum, to the substrate. Although this behaviour was never observed as a discrete unit, but in conjunction with other units, usually upright or semi-upright, it appeared to represent a perineal drag, as occurs in many other rodents (Eisenberg 1962, 1967; Ewer 1968; Happold 1973, 1976).

O. irroratus frequently urinated at regular sites, which suggests marking (Davis 1972), and defaecated more or less at random, but R. pumilio often performed the two functions at specific points, and both may serve as marks (Marais 1974). Johnson (1980) notes that during perineal drag R. pumilio deposits droplets of urine on the substrate, which suggests an immediate transfer of information rather than marking (see section 4.4.1). P. natalensis did not use specific points for defaecation or urination, and is known to remove faeces from nest-boxes and dispose of them (Cilliers 1972), while faecal pellets are rarely found in their burrows (Schultz 1951, in Veenstra 1958). None of the species displayed great interest in conspecific faeces or urine, possibly also because of residual odour.

Visual communication, implied by postural changes and adjustments to the disposition of various external organs, occurred in all three species. These signals are summarized in Table 18, but their functions are expanded upon in sections 4.3.2-4.3.5. Although movements of the fore-paws were used by all three species to physically ward off adversaries, hence providing tactile cues (below), the paws often did not come into contact

Table 18. Visual communication in O. irroratus, R. pumilio and P. natalensis: movements associated with aggressive (A) and defensive agonism (D) and amicable interaction. N represents "normal", and infers posture or organ disposition to be indistinguishable from that in solitary animals.

SPECIES	BEHAVIOURAL STATE		GROSS SIGNALS			SUBTLE SIGNALS			
			Body	Fore-paws	Tail	Eyes	Ear pinnae	Face	Pelage
OTOMYS	AGONISTIC	A	Upright	Vigorous warding	Stiff or violently quivered	N	N or slightly forward	Not averted	N or slight pilo-erection
		D	Upright	Vigorous warding	N	N or narrowed	N or slightly flattened	Not averted	N
	AMICABLE		Quadrupedal	N	N	N	N	Seldom averted	N
RHABDOMYS	AGONISTIC	A	Quadrupedal or upright	Warding	Stiff or quivered	Dilated	N or forward (extreme)	Not averted	Extreme pilo-erection
		D	Quadrupedal or upright	Feeble warding	N	Narrowed or closed	Flattened	Slight aversion	N
	AMICABLE		Quadrupedal or semi-upright	N	N	Narrowed or closed	N or flattened	Extreme aversion	N

Continued overleaf

Table 18. Continued.

SPECIES	BEHAVIOURAL STATE		GROSS SIGNALS			SUBTLE SIGNALS			
			Body	Fore-paws	Tail	Eyes	Ear pinnae	Face	Pelage
PRAOMYS	AGONISTIC	A	Quadrupedal or upright	Warding	Stiff or quivered	N	Variable	Slight aversion	N or slight pilo-erection
		D	Quadrupedal or upright	Feeble warding	N	N or narrowed	Variable	Slight aversion	N
	AMICABLE		Quadrupedal or semi-upright	N	N	N or narrowed	Variable	Extreme aversion	N

with the other animal, so that warding movements must be regarded as also providing visual information. Visual signals appeared to fall into two categories, those involving large-scale or gross changes in body posture and vigorous movements of the fore-paws and tail, and those that were more subtle, namely changes in the disposition of the eyes, ear pinnae, face and pelage (Table 18). Although most of the recognizable units were present in all three species, P. natalensis appeared in general not to emphasize visual signalling, while O. irroratus and R. pumilio did so, but in different ways. R. pumilio displayed extreme lability of the eyes, ears and pelage, and of the position of the face, while in O. irroratus signals in the other (gross signals) category were well developed. In addition to drawing the body upright and fore-paw and tail movements, aggressive O. irroratus also employed a lateral display (a slight turning to one side during advance; Davis 1972), a probable adaptation to enhance the apparent size of the animal. Ear movements in P. natalensis were so variable that their function in communication was difficult to assess, and unlike R. pumilio, and to some extent O. irroratus, it was impossible to use the position of the pinnae as an indicator of behavioural state.

An estimate of species-specific emphasis of auditory, olfactory and visual communication was obtained by scoring the recognizable units on the basis of relative development in the three species (Table 19). Auditory communication is included in this analysis although the auditory repertoires of the three species are certainly more complex than suggested by the number of units identified here (see above). Scores of three, two and one were respectively allocated to highly, moderately and poorly developed units, and no score was given where units were entirely absent. The distributions of these scores between the three species were compared for each category using Kruskal-Wallis one-way AOV by ranks (section 2.5).

Table 19. Emphasis of auditory, olfactory and visual communication in *O. irroratus*, *R. pumilio* and *P. natalensis*. Scoring: 3 = well developed; 2 = moderately developed; 1 = poorly developed.

	FUNCTIONAL UNITS	*O. irroratus*	*R. pumilio*	*P. natalensis*
AUDITORY	Loud "chit"	3		
	Alarm squeal	3		
	Squeak		1	
	Muted squeak			1
	Muted "cheep"			1
	Tail-quiver	3		
	Tooth-chatter		1	
	TOTAL SCORE	9	2	2
OLFACTORY	Cheek-rub	1		2
	Chin-rub		1	2
	Neck-rub			2
	Naso-anal contact	1	1	3
	Genital presentation			3
	Perineal drag	3	3	3
	TOTAL SCORE	5	5	15
VISUAL	Body upright	3	1	1
	Warding	3	1	1
	Face aversion	1	3	3
	Eye disposition	1	3	1
	Ear pinna disposition	1	3	
	Tail disposition	3	1	1
	Pilo-erection	1	3	1
	Lateral display	3		
	TOTAL SCORE	16	15	8

This test gives some weight to zero scores (Table 19) so that the values of H (below) represent the minimum probabilities of statistical significance. The distributions were significantly different in the case of olfactory communication, where P. natalensis scored most highly (H_2 = 6.41; P<.05), but were not significantly different in either the auditory (H_2 = 0.94; P>.05) or visual (H_2 = 3.12; P>.05) categories. However, a number of numerical if not statistical differences were present in the auditory and visual distributions. On the basis of these scores, O. irroratus appeared to utilize auditory signalling to a far greater extent than either R. pumilio or P. natalensis, and P. natalensis to utilize visual communication to a far lesser extent than either O. irroratus or R. pumilio.

The role of tactile communication is difficult to assess, but such activities as allogrooming, huddling, and resting in contact in or out of a nest-box (section 4.3.4) may be assumed to strengthen social ties. Representatives of all three species engaged in this contact-promoting behaviour, but allogrooming was most typical of P. natalensis. Similarly, in agonistic situations all three species warded off opponents with the fore-paws (section 4.3.3). This activity presumably transmits information regarding relative strength and aggression, particularly in O. irroratus where the movements are highly co-ordinated and exert considerable force. The robust courtship behaviour of male R. pumilio, in which unreceptive females were persistently jostled and mounted, may provide tactile stimuli which are partially responsible for rapid onset of oestrus in this species (section 4.3.5).

4.3.2. Initial contact behaviour

Initial contact was naso-nasal in all three species and followed slow,

elongate approach with the body low and the tail held stiffly clear of the substrate. O. irroratus displayed potential agonism during approach, which tended to be hesitant and in a posture indistinguishable from aggressive approach (section 4.3.3). One of the animals would often break off to avoid the other before contact was made, while in some cases agonistic sequences were entered into prior to investigatory contact. In contrast, approach in P. natalensis was more direct and essentially amicable, and although some particularly aggressive animals reacted agonistically, most dyads followed naso-nasal contact by mutual sniffing of the face and neck, and in many cases the ano-genital region. Approach in R. pumilio was similarly direct, but was neither overtly aggressive nor amicable, and the posture was interpreted as being neutral. Contact between male R. pumilio was at times immediately followed by agonistic sequences, and in intersexual dyads male amicability or sexual interest was commonly responded to by low intensity aggression by the female.

4.3.3. Agonistic behaviour

Sixteen functional units of agonistic behaviour were identified. The names of these behaviour patterns are largely self-explanatory, and in general only details of their occurrence are given (Table 20). In this table units have been paired where expression of one was specifically dependent on that of another (viz. flight and chasing; attack and fighting; nest attack/defence; nest-guarding/restriction). In addition, the units have been scored as in the communication analysis (section 4.3.1), on the basis of relative development in the three species (Table 21).

Predictably, all three species displayed a caste-specific gradation in potential aggression as follows: scrotal male > perforate female > non-scrotal

Table 20. Agonistic behaviour in O. irroratus, R. pumilio and P. natalensis. Symbols following the names of the functional units indicate whether the behaviour was used by an aggressor (A) or a non-aggressor (N).

FUNCTIONAL UNITS	COMMON TO ALL SPECIES	O. irroratus	R. pumilio	P. natalensis
AVOIDANCE (N)	Remaining in nest-box or hiding at ground level.		Hiding arboreally or attempting to escape from cage.	
MUTUAL AVOIDANCE (A & N)	Both animals avoiding close approach.	In direct conflict situations both animals breaking off and moving away from one another.		
AGGRESSIVE APPROACH (A)	Slow approach, with tail clear of substrate, either stiffly held or quivering.	Body low and elongate, with ears slightly forward and pilo-erection restricted to neck or absent; tail sometimes quivering on substrate, throwing soil about; occasional lateral display during advance; seldom resulting in attack on non-aggressor.	Hunched posture with perineal drag, eyes dilated, ears forward, and extreme pilo-erection; aggressors often attacking non-aggressors if they did not flee; perineal drag previously reported in aggressive R. pumilio (Marais 1974), and as "masturbatory scrotum dragging" in males (Choate 1972).	Body low and elongate, with pilo-erection restricted to neck or absent; rarely followed by attack on non-aggressor.
FLIGHT AND CHASING (A & N)	Usually following aggressive approach, with aggressor attempting to bite tail or rump of fleeing non-aggressor.	Flight usually direct to nest-box; followed by nest attack/defence sequences; escape-leaping rare.	Flight rarely to nest-box; flight/chasing sequences often protracted, with non-aggressor escape-leaping when cornered; at times resulting in locked fighting.	Flight often direct to nest-box, but sustained running about the cage, with frequent escape-leaping not unusual; locked fighting occasionally resulting.

Table 20. Continued.

FUNCTIONAL UNITS	COMMON TO ALL SPECIES	O. irroratus	R. pumilio	P. natalensis
DEFENSIVE THREAT (N)	Warding with fore-paws.	Upright posture accompanied by vigorous warding and loud "chits"; defensive threat highly aggressive, and almost invariably preventing attack by aggressor.	Upright posture, but seldom utilized; feeble warding accompanied by tooth-chattering, with ears flattened and eyes narrowed or closed; rarely preventing attack by aggressor.	Semi-upright posture, with feeble warding and muted squeaking; readily transmuted into submission, usually preventing attack by aggressor.
UPRIGHT SPARRING (A & N)	Upright posture, including warding; injury rare and superficial.	Well developed, even in greatly outweighed non-aggressors; accompanied by loud "chits" and vigorous warding; aggressor leaning forward to lunge at and jostle non-aggressor; non-aggressor more upright or leaning backward; may establish relative dominance (Davis 1972).	Uncommon bouts, transitional between aggressive approach and flight/chasing or fighting; usually between well matched animals, with both attempting to bite; termed "boxing" by Marais (1974).	Warding accompanied by head-weaving, with each attempting to get under the other's guard; biting unusual; normally in a well matched dyad, with less forceful animal (non-aggressor) eventually omitting head and fore-paw movements, and submitting to being groomed.

Continued overleaf

Table 20. Continued.

FUNCTIONAL UNITS	COMMON TO ALL SPECIES	O. irroratus	R. pumilio	P. natalensis
SUBMISSION (N)		Almost invariably following upright sparring, with non-aggressor falling onto its side with body twisted and arched, its hind feet remaining in contact with the substrate, while it continues to face the aggressor; accompanied by vigorous warding and loud alarm squealing; non-aggressors maintain a high level of aggression, even if greatly outweighed; submissive non-aggressors rarely attacked.	Normally in response to amicable approach by former aggressor; quadrupedal posture, with ears flattened, eyes narrowed or closed, and face averted to permit head and neck to be sniffed; slight pilo-erection in some cases; submissive behaviour ineffective in preventing attack following aggressive approach; recorded as being a rare behaviour (Johnson 1980).	Usually following upright sparring; semi-upright or quadrupedal posture, with eyes sometimes narrowed and face almost invariably averted to permit sniffing and grooming; submissives rarely attacked.
ATTACK AND FIGHTING (A & N)	Generally uncommon, and serious injury rare in observation cages ($0.72m^2$).	Generally in an angled head to head position, following non-aggressor turning to face aggressor when cornered; damaging fights usual between animals (even males and females) housed together in holding cages ($0.125m^2$).	Head to tail position most usual, following aggressor biting tail or rump of fleeing non-aggressor and "hanging-on" (Marais 1974); animals locking together following non-aggressor turning to defend itself; fighting uncommon in holding cages.	Head to tail position usual (explanation as for R. pumilio); most bites in P. natalensis inflicted posteriorly (Cilliers 1972); fighting rare in holding cages.

Continued overleaf

Table 20. Continued.

FUNCTIONAL UNITS	COMMON TO ALL SPECIES	O. irroratus	R. pumilio	P. natalensis
NEST ATTACK/ DEFENCE (A & N)	Aggressor attempting to enter nest-box occupied and defended by non-aggressor.	Well developed nest attack behaviour, including vigorous attempts to enter nest-box or dig out occupant; nest defence equally well developed, with non-aggressor warding off intruder with fore-paws; accompanied by both animals "chitting" loudly; sequences often prolonged; aggressor rarely able to enter.	Well developed nest attack involving aggressor moving rapidly about nest-box entrance and suddenly rushing past non-aggressor into box; in spite of non-aggressor attempting to bite, aggressor rarely prevented from entering; sequences usually brief; occupant usually driven from box and pursued.	Nest attack and defence similar to O. irroratus, but aggressive P. natalensis less forceful, with no attempts to dig out non-aggressor; vocalization limited to muted squeaking by non-aggressor; aggressor seldom able to enter.
NEST GUARDING/ RESTRICTION (A & N)		Guarding behaviour of aggressor lying 30-50cm from occupied nest-box and occasionally "chitting" or going up to investigate entrance, commonly restricts non-aggressor to nest for several hours at a time.	These units lacking from R. pumilio agonistic inventory; nest-box utilization frequently avoided by non-aggressor (also noted by Marais 1974).	Nest guarding/restriction sequences functionally indistinguishable from O. irroratus but aggressive P. natalensis less overtly agonistic, lying approximately 10cm from entrance and silently going up to sniff it every few minutes; maximum observed restriction of non-aggressor to nest-box was 32 minutes.

Continued overleaf

Table 20. Continued.

FUNCTIONAL UNITS	COMMON TO ALL SPECIES	O. irroratus	R. pumilio	P. natalensis
FOOD THEFT (A)		Occasional sorties by nest-restricted non-aggressors to drag food (e.g. carrot) into nest often thwarted by aggressor reaching it first and dragging it away.		
"DEFEAT" POSTURE			Sitting in hunched posture with head lowered, fur erect, ears flattened and eyes narrowed or closed; similar to Rattus (Steiniger 1950).	

Table 21. Emphasis of units of agonistic behaviour in O. irroratus, R. pumilio and P. natalensis. Scoring: 3 = well developed; 2 = moderately developed; 1 = poorly developed.

FUNCTIONAL UNITS	O. irroratus	R. pumilio	P. natalensis
Avoidance	1	3	1
"Defeat" posture		3	
Mutual avoidance	3	2	1
Aggressive approach	3	3	2
Flight	2	3	2
Chasing	2	3	2
Defensive threat	3	1	1
Upright sparring	3	1	2
Submission	3	3	3
Attack	2	3	2
Fighting	2	3	1
Nest attack	3	2	1
Nest defence	3	1	1
Guarding	3		1
Nest restriction	3		1
Food theft	3		
TOTAL SCORE	39	31	21

male > imperforate female. In intracaste situations, the heavier animal was normally the more aggressive.

Distribution of scores obtained by the three species for agonistic behaviour (Table 21) were significantly different ($H_2 = 9.90$; $P<.05$). O. irroratus was superficially the most aggressive of the three species, possessing all but one of the identifiable units of agonistic behaviour, of which 10 were well developed, and obtaining the highest total score (Table 21). P. natalensis was least aggressive in terms of total score, and although 14 units were present, most were poorly developed. R. pumilio possessed only 13 units, but eight of them were well developed, and this species was the most directly aggressive, readily engaging in behaviour which resulted in potentially damaging fights. Locked fighting is less frequently engaged in by bipedal than by fully quadrupedal heteromyids (Eisenberg 1963), and a similar trend was apparent in my study, with R. pumilio, the species least often engaging in body uprights, most often resorting to locked fighting. In contrast, O. irroratus had highly developed behaviour inhibiting attack and fighting, although they did occur from time to time. Neither aggressive nor defensive agonism was highly developed in P. natalensis. All three species possessed well developed submission behaviour, but whereas this was normally sufficient to prevent attack by aggressive O. irroratus and P. natalensis, aggressive R. pumilio frequently attacked submissives, suggesting that ritualization of aggression is poorly developed in this species (section 4.4.2).

Fighting to the death was rare in the laboratory. However, one O. irroratus female was killed by another female in an observation cage ($0.72m^2$), but serious injury was far less common than in holding cages ($0.125m^2$), where even intersexual dyads could generally not be housed

without the risk of one animal being killed. Davis (1973) likewise records captive O. irroratus fighting to the death. Although one male R. pumilio was killed by another male in an observation cage, serious injury was unusual. Fighting was sufficiently uncommon in holding cages to allow housing R. pumilio together in dyads or larger groups, and although fatal wounding occurred it was usually as a result of competition between males for an oestrus female, as noted by Choate (1972), who also records particularly aggressive males killing oestrus females. However, confining R. pumilio at high density in a 36m² enclosure showed that although both intra- and intersexual fighting occurred, wounding was restricted to mature males (Marais 1974). In contrast, P. natalensis rarely inflicted wounds, even in small cages, although Cilliers (1972) records a single male killing four other males and three females over a period of three months, reducing the population in a 3.4m² enclosure to three animals, the male and two females.

4.3.4. Amicable behaviour

Five units of contact-promoting behaviour were represented in all three species (Table 22), with the major interspecific differences quantitative (section 5) rather than qualitative. In view of the small number of units and the similarities of expression, no attempt has been made to estimate species-specific emphasis of amicable behaviour. However, three major interspecific differences were observed. While amicability was developing, approach behaviour in O. irroratus and P. natalensis was almost indistinguishable from aggressive approach (section 4.3.3) but in R. pumilio the postures were clearly different. In addition, whereas recognition contact in R. pumilio and P. natalensis was either quadrupedal or semi-upright, in O. irroratus it was invariably quadrupedal. Finally

Table 22. Amicable behaviour in O. irroratus, R. pumilio and P. natalensis.

FUNCTIONAL UNITS	COMMON TO ALL SPECIES	O. irroratus	R. pumilio	P. natalensis
AMICABLE APPROACH	During development of amicability approach slow and cautious with body elongate and tail held normally or stiffly, clear of substrate; some animals fleeing at such approach by formerly aggressive partner. Once complete amicability developed, approach direct, without overt nervousness in either animal.	Response often aggressive (e.g. defensive threat; section 4.3.3) during development of amicability.	Tail at times undulating slowly approximately 1cm from substrate; response usually submissive.	Response either submissive or immediately amicable.
RECOGNITION CONTACT	Almost invariably naso-nasal, with mutual sniffing of face and surrounding areas.	Quadrupedal; face-aversion seldom observed, and then very slight, eyes and ear pinnae normal.	Quadrupedal or semi-upright; face-aversion by former non-aggressor to permit sniffing by partner; neck at times twisted so that head is partially inverted, but decreasingly extreme with increasing familiarity; eyes usually narrowed or closed and ears flattened.	Quadrupedal or semi-upright; face-aversion as in R. pumilio, but less extreme; naso-anal investigation often following naso-nasal contact; eyes sometimes narrowed, but ear position variable.

Continued overleaf

Table 22. Continued.

FUNCTIONAL UNITS	COMMON TO ALL SPECIES	O. irroratus	R. pumilio	P. natalensis
HUDDLING	Normally an extension of recognition contact, and interspersed with bouts of allogrooming or mutual grooming.	Animals sometimes feeding with bodies in contact.		
ALLOGROOMING AND MUTUAL GROOMING	Maximum grooming attention to head, neck and dorsum.	Allogrooming at times accompanied by holding partner's face in the fore-paws.	Partner at times held down to be groomed, but common only in intersexual dyads.	Partner occasionally held down to be groomed.
NEST-SHARING	Once relationships completely amicable, but responses variable from dyad to dyad.			

O. irroratus were never observed to hold down a partner while grooming it, thereby adopting a bipedal posture, but the other two species from time to time did so.

4.3.5. Sexual behaviour

Reproductive activity in O. irroratus breaks down in captivity (Davis 1973), and there are no existing records of this species breeding in the laboratory. A single litter was conceived in captivity during the present study, but although the male was removed before parturition in the hope that this would improve the chance of the young surviving, they were killed by the mother shortly after birth. Mating behaviour was not observed, and apparent sexual behaviour was limited to a single act in which a female approached a male without the usual naso-nasal recognition contact (section 4.3.4), sniffing and nuzzling the base of the tail and scrotum. The male did not respond.

R. pumilio and P. natalensis breed freely in the laboratory, and sexual behaviour was observed without difficulty. Courtship and mating in the two species are described in Table 23.

Important differences were apparent in both courtship and mating behaviour in the two species (Table 23). During courtship, visual "display" by sexually aroused males was typical of R. pumilio, but in P. natalensis olfactory cues appeared more important. This was predictable in view of the apparent emphasis of visual communication in R. pumilio, and of olfactory communication in P. natalensis (section 4.3.1). Courtship intensity was extremely high in R. pumilio, and on occasion resulted in copulation within 15 minutes of animals meeting for the first time, but in

Table 23. Sexual behaviour in R. pumilio and P. natalensis.

FUNCTIONAL UNITS	COMMON TO BOTH SPECIES	R. pumilio	P. natalensis
COURTSHIP	MALE: Initiating most sexual contact, and performing most allogrooming, as in many other rodents (Dewsbury 1975); allogrooming attention mainly to female genital region; frequent attempts to mount even unreceptive females. FEMALE: Often moving off during courtship; at times lifting tail to permit male sniffing and nuzzling genital region.	MALE: Approach direct; similar to aggressive approach (section 4.3.3) with pilo-erection and perineal drag; movements rapid and jerky; female moving off during courtship, closely followed. FEMALE: Rarely making sexual approaches to male; repeatedly moving off at high speed with male following; tail-lifting only in receptive females; copulation often within five minutes of commencing tail-lifting.	MALE: Approach rapid and direct in hunched posture with perineal drag and slight pilo-erection; often presenting rump to be sniffed and nuzzled by female; female moving off during courtship often not followed. FEMALE: Relatively frequently soliciting male sexual attentions, but then moving unhurriedly away with male at times following; tail-lifting common even several days prior to oestrus; solicitation involving sniffing and nuzzling male genital region, and presenting rump, as in male.
MATING	MALE & FEMALE: Female adopting lordosis posture in response to being mounted and gripped round flanks, thus permitting intromission and copulation of 1-2 seconds' duration.	Copulatory sequences relatively protracted (up to 17 intromissions in approximately 15 minutes); females tending to move off between intromissions, but closely attended by male.	Copulatory sequences relatively brief (up to six intromissions in approximately two minutes).

some cases where mating did not occur within two or three days males tended to lose interest, and courtship ceased. In P. natalensis the course of events was always slower, with courtship recurring intermittently for at least 48h, and in some cases for a week or more before copulation was achieved. Frequency of copulation was far greater in R. pumilio than in P. natalensis, but I did not undertake detailed study of copulatory patterns to ascertain, for instance, the stage at which sperm transfer occurred (Dewsbury 1975, 1979), so that extrapolation from this difference is impossible.

4.4. Discussion

The social inventories of O. irroratus, R. pumilio and P. natalensis show broad similarities. Behavioural analogues may result from persistence of basic rodent characters or close taxonomic affinities (Happold 1976), but Wilson (1975) suggests that the coarse nature of behavioural nomenclature frequently results in functionally discrete behaviour patterns being included under the same name. However, in a comparative study of the present nature it seems unlikely that functional analogy would be ascribed in error, and since the three species are not closely related (section 1.2.2) it is probable that behavioural similarities at least partially reflect character persistence (i.e. persistence of basic rodent characters). Moreover, basic similarities were predictable in view of the degree to which the ecological niches of the three species overlap (section 1.2.5).

Behavioural postures are transmutative (Eisenberg 1962), and although behavioural states (Altmann 1974) often remained unaltered for considerable periods in this study, the units comprising each state generally formed a

rapidly changing continuum. Intraspecific differences in social responses tended to be quantitative, and were largely dependent on the sex, reproductive condition and/or mass of one animal relative to its partner (section 5). Qualitative disparities were similarly influenced by dyadic partners, and although small behavioural differences may be important in highly detailed studies (e.g. Dewsbury 1975, 1979), I found all behaviour other than that relating to sex (section 4.3.5) to be available to all castes.

Discussion in the following sections on communication (4.4.1), agonistic behaviour (4.4.2) and sexual behaviour (4.4.3) excludes consideration of environmental influences on social behaviour; this aspect is dealt with under Social Ecology (section 6).

4.4.1. Communication

In general, communication in O. irroratus, R. pumilio and P. natalensis appears to be dominated respectively by the auditory, visual and olfactory senses (section 4.3.1). Although Davis (1973) suggests that O. irroratus relies most strongly on olfaction, my observations support Kingdon (1974) who states that in Otomys auditory communication is of overriding importance. The position of the ear pinnae in P. natalensis was highly variable, and was not a reliable indicator of behavioural state. The frequency with which ear position was changed suggested that adjustments were being made to improve auditory perception, and this species may, in addition to possessing extreme olfactory acuity, emphasize ultrasonic signalling, as suggested by D.H. Gordon (Pers. comm.). R. pumilio may be less dependent than P. natalensis on communication of this type, since ultrasounds are associated with only three types of behaviour, all of them agonistic (section 4.3.1), and were emitted only by a non-aggressor attempting to

appease an aggressor (Johnson 1980).

Marais (1974) noted that R. pumilio is able to follow a conspecific scent trail, implying well developed olfactory capabilities, and it is likely that O. irroratus is similarly endowed. The majority of rodents apparently depend largely on olfactory communication (Eisenberg 1962, 1963; Barnett 1963; Ewer 1968), but it is obvious that further information is required on both auditory and olfactory signalling in the three species under consideration here before final conclusions can be reached in respect of their systems of communication.

4.4.2. Agonistic behaviour

Behaviour inhibiting closing with and actually fighting a rival appears to be better developed in O. irroratus and P. natalensis than in R. pumilio (section 4.3.3). In addition, O. irroratus did not employ the typically aggressive upright posture during amicable interaction, or hold a partner down while grooming it, while the other species did both (section 4.3.4), and it seems likely that the lack of uprights in the O. irroratus amicable inventory is related to avoidance of conflict. Non-aggressive R. pumilio tended to flee rather than threaten or submit, so that fighting in free-living societies is probably rare. In addition, this species was the only one in which non-aggressors vigorously attempted to escape from the cage in agonistic circumstances, and to adopt a "defeat" posture (Steiniger 1950), which suggests that in conflict situations a strong urge exists to withdraw.

The above suggests that whereas O. irroratus and P. natalensis have evolved partially ritualized agonistic repertoires, R. pumilio has not.

However, agonistic buffering (Crook et al 1976) appears to occur in all three species. Animals do not usually engage in potentially lethal combat, but rather attempt to drive competitors away or establish superiority, thereby ensuring dispersion to optimum species-specific density levels, and reducing fights to a minimum. These requirements have necessitated retention of aggression even in mammals in which damaging fights are rare (Eibl-Eibesfeldt 1962), and have been accomplished by adaptive ritualization of conflict in many species (Hinde 1966). O. irroratus and P. natalensis appear to have evolved signals which minimize damaging intraspecific conflict, as reported in a number of rodents (Eibl-Eibesfeldt 1962; Eisenberg 1962; Ewer 1968), while R. pumilio apparently falls into a non-ritualized category in which aggression tends to be direct, and in which non-aggressors are attacked but readily escape (Eibl-Eibesfeldt 1962).

The different patterns relating to nest-box occupation, in which non-aggressive O. irroratus and P. natalensis were normally able to defend the entrance against an aggressor, but R. pumilio was not (section 4.3.3), presumably also relate directly to ritualization of aggression.

4.4.3. Sexual behaviour

Sexual behaviour in R. pumilio was considerably more intense and energy consuming than in P. natalensis, but was generally compensated for by rapid achievement of copulation (section 4.3.5). Females usually require specific courtship behaviour by males prior to copulation (Trivers 1972), and may be stimulated to accelerate onset of oestrus (Ewer 1968), which was apparently the case in R. pumilio. The rate at which free-living animals are likely to meet may determine the reproductive strategy of the

male (Parker 1974), and conversely, reproductive time investment is likely to be an indicator of species-specific modes of dispersion. Hence, the disparity in reproductive strategies of R. pumilio and P. natalensis seems to relate to their respective social systems (sections 5.4.2.2, 5.4.2.3). Moreover, Dewsbury (1975) suggests that species in which copulation is rapidly initiated are unlikely to be monogamous, so that R. pumilio would be expected to mate promiscuously, while P. natalensis may tend toward pair-bonding and concomitant monogamy.

5. SOCIAL ORGANIZATION

5.1. Introduction

Modes of dispersion and related phenomena in animal societies are determined by social organization, which is itself determined by inter-individual social behaviour of conspecifics (Crook 1965; Happold 1973, 1976; McBride 1976) between which reciprocal communication and co-operation occur (Happold 1973, 1976; Wilson 1975). In general terms, social systems fit recognizable species-specific patterns (McBride 1976), but they are subject to both intrinsic (genetic) and extrinsic (environmental) influence and are dynamic in space and time (Crook 1970; Happold 1973, 1976; Wilson 1975; Crook et al 1976). Hence, social organization is capable of evolutionary selection and should therefore be adaptive (Barash 1974), even though the individuals comprising a society may act to maximize their own inclusive fitness (Hamilton 1964; Maynard Smith 1964; Wilson 1975; Dawkins 1976; Barash 1977).

The social organization continuum is represented at one extreme by dispersed or solitary systems in which animals may physically associate together only to mate, and at the other by cohesive, highly integrated systems of inherently sociable species. However, all social systems appear to have a number of characteristics in common, although there is no consensus regarding definition of the essential qualities of sociality.

Happold (1973, 1976) recognised the following essential components of mammalian social organizations: COMMUNICATION - a prerequisite of sociality; CO-OPERATION - individual contributions toward the adaptive goal of the species; DISPERSION AND TERRITORIALITY - products of mutual repulsion

engendered by agonistic behaviour; COHESION- the result of mutual attraction promoted by amicable behaviour. Wilson (1975) listed 10 qualities of social organization, the majority of which were directly related to communication. Crook et al (1976) classified mammalian social systems into 12 sociotypes on the basis of mating, rearing and grouping, and dispersion strategies. In an attempt to provide a standardized method of describing social organization, McBride (1976) compiled a lengthy questionnaire to facilitate summarizing available information on sociality in particular species.

Accepting Wilson's (1975, p.16) warning that "classification based on all relevant traits is a bottomless pit", the methodological approach to the present study was kept as simple as possible. Happold (1973, 1976) used the following parameters to catagorize social organization: CAPTIVE ANIMALS - types of relationships (attracting or repelling), occurrence of communal nesting, and duration of the pair-bond as indicated by communal nesting during pregnancy, parturition and lactation; FREE-LIVING ANIMALS - number, ages, and sexes of animals found together in nests or burrows. I adapted Happold's captive study parameters to my own requirements (section 5.2.2). However, field conditions (e.g. vegetation density; section 3.3.3.1) and the fact that O. irroratus and R. pumilio nest on the surface (section 1.2.6) made it impossible to use her field parameters in the present study. Hence, an alternative method of estimating sociability in free-living societies was developed (section 5.2.1).

Studies of small mammal social organization normally fit into one of three categories. First, post-natal development studies may include description of social ontogeny from birth to sexual maturity, and of parent/young relationships (e.g. Williams & Scott 1953; Davis 1972, 1973; Brooks 1972, 1974; Baker & Meester 1977; Willan & Meester 1978), although

there is a tendency for little detail to be available on the juvenile period (weaning to sexual maturity; Williams & Scott 1953). Second, some investigations deal almost exclusively with adult interaction (e.g. Eibl-Eibesfeldt 1962; Eisenberg 1962, 1963, 1967). Third, attempts have been made to describe social organization in integrated rodent societies, as for example in studies on Marmota (e.g. Barash 1974; Armitage 1977).

A valuable contribution to the understanding of differentiation of social roles was provided by Wilson (1973) in which she showed that differences in the social environment of sexually immature Microtus agrestis of full adult size may be reflected in the population cycle of the following year. The broad implications of these findings led me to include 10 caste combinations of each species in the captive study, and to analyse trapping data in terms of 21 caste combinations (section 2.2). Further, an overview of the effects of the sex and reproductive condition of adults on sociability was obtained by analysing data so as to treat these factors separately.

5.2. Methods

5.2.1. Field studies

O. irroratus and R. pumilio were trapped at the Dargle grassland study area, and P. natalensis at Darvill (sections 2.3, 3.2.1.1), using the methods outlined in section 3.2.1.2.

From trapping data, estimates were made of overall association and of association in 21 caste combinations (section 2.2) of each species. A

simple formula was used to calculate indices of association (A), expressing an assumed relationship between the number of dyadic associations for a particular caste combination (a), the mean total captures for the castes they represented (c), and the mean time interval between associated captures (h):

$$A = \frac{a \times 10^3}{c \times h}$$

Dividing by c x h expresses the assumption that greater affinity was indicated by a greater proportion of dyadic associations in comparison to the number of available animals, and by a smaller time interval between associated captures. The maximum interval (h) permitted in this analysis was 48h, and only animals trapped at the same or adjoining trap-stations (vertically, laterally or diagonally adjoining) within this period were regarded as associated. Captures which did not fall within these limits were regarded as isolated from one another. The rationale of using indices of association as defined here is set out below.

Animals captured at the same or adjoining trap-stations may be assumed to be associating with one another (Happold 1973, 1976), but cumulative mapping of captures made during discrete trapping sessions may be of little value since the size and position of home ranges and centres of activity may change with time (Brant 1962; Brown 1966; Jewell 1966). Hence, associations in a free-living society form a continuum in space and time. The criterion of capture at the same or adjoining stations was qualified by the condition that no more than 48h separated any two captures regarded as associated (above) on the grounds that the probability that scent marks or other signs will be detected by a conspecific decreases with time. At least some secretions lose most of their potency within 12-24h (Johnston

1974), which explains repeated marking by mammals (Ewer 1968; Johnson 1973, 1975; Johnston 1975). In the absence of more specific evidence regarding the temporal qualities of remote signals such as scent marks (see section 6.2.1), the 48h period was selected as providing a good compromise between almost certain association (i.e. simultaneous capture at the same station) and a far lower probability of association (e.g. capture at adjoining stations in different months).

The use of indices of association, as defined here, has certain advantages: whereas assessment of modes of dispersion by home range mapping requires at least 10 (Flowerdew 1976) or 15 (Stickel 1954) captures/animal, the method I have used requires only one, as in removal trapping, for example. This maximizes the useful data obtained from small numbers of captures, and permits joint treatment of data from different types of trapping (section 3.2.1.2). In addition, the difficulty of assessing the role of transients (Brant 1962; Jolly 1965) is overcome. The interpretation of association between two animals, depending as it does on an "on/off" situation, is such that immigration and emigration are irrelevant to the analysis, and transients are regarded as part of the social complex at the time they were captured. However, the indices are capable of only non-parametric statistical comparison.

5.2.2. Captive studies

Caging and maintenance, and the conditions under which the study was undertaken are described in sections 2.4.1 and 2.4.2. Interaction of four conspecific dyads of each of 10 caste combinations (section 2.2) was studied in neutral arena encounters (Eisenberg 1967; Happold 1973, 1976) for 5h/dyad (section 2.4.2). Additional encounters were staged between scrotal males and pregnant or lactating females of each species. Dyads which had not

previously met in the laboratory were selected as available, and each animal was used twice, each time in combination with a member of a different caste. Encounters were started one hour after the start of the appropriate part of the light cycle (section 2.4.2), and subsequent observation periods were at the same time on successive days. Before an encounter the subjects were weighed and placed in separate nest-boxes together with nesting material from their holding cages, and confined there for 30 minutes so that the new nest became associated with the home-cage environment (Happold 1973, 1976). Nest-boxes were then opened, giving the occupants access to the arena (living area) of the cage. Interaction was observed for the first hour and for one hour daily for the next four days. In addition, observations were made of dyads or larger groups, usually a male, female and one or more litters of different ages, in holding cages in the animal house (section 2.4.1).

One-zero scoring with 10-second time intervals was used to record frequencies of agonistic, amicable and sexual interaction directly on record sheets. One-zero scoring was selected as it couples convenience with relatively low bias (below).

It is important to accurately define the scoring method used in behavioural studies (Altmann 1974). In one-zero scoring the absolute time spent in a particular behaviour is not recorded, but rather the number of intervals (in this case 10-second intervals) which include any amount of time spent in that behaviour. If more than one behaviour occurs in a single interval only the first is scored; equally, if the same behaviour occurs more than once in the same interval it is scored only once. Simpson & Simpson (1977) have criticised one-zero scoring, as has Altmann (1974, p.253) who suggests that the number of intervals scored for a behaviour is

the "upper bound" on time actually spent in that behaviour. Dunbar (1976) empirically tested one-zero scoring against actual time spent in a particular short-duration behaviour, and found that use of 5- and 15-second time intervals produced over-estimations of 6.0% and 17.3% respectively. Use of intervals of one second or less, although impracticable, can be assumed to produce errors approximating zero. The relationship between a hypothetical error of zero using one-second intervals and Dunbar's (1976) errors is practically linear, and it may be assumed from this that for 10-second time intervals an error of 11-12% would have occurred. It follows that bias of this order of magnitude may be present in my study, with over-estimation of short-duration units (above) and, hence, under-estimation of units of longer duration. However, sample sizes were large enough (i.e. a total of 432 000 one-zero scores) for it to be expected that errors would generally have nullified one another.

Happold (1973, 1976) combined data for each dyad, thereby implying absolute reciprocity between interacting animals, but the qualitative study (section 4) showed that although behavioural states were normally interdependent, they were frequently at least briefly independent. Similarly, frequencies of interaction were often partially independent, since potentially social acts by one animal were not always responded to by the other. In an attempt to obtain a quantitative assessment of differences in the social potential of animals of different size, sex and reproductive condition, frequencies were recorded separately for the two animals comprising each dyad. However, X^2 (contingency table) analysis showed that none of the above differences were statistically significant for any dyad. Accordingly, unless otherwise stipulated, the results given in section 5.3.2 represent meaned data for each encounter.

The variable matrix resulting from use of the methods described above is large and unwieldly, and interpretation of results has been difficult.

A portion of this matrix is given in Table 24 (viz. that for four replications of O. irroratus scrotal male/scrotal male encounters, each involving five observation periods). Illustration of the variable matrix for the entire study would have necessitated duplication of columns 3 and 4 (Table 24) for the remaining nine O. irroratus caste combinations, and duplication of columns 2, 3 and 4 for R. pumilio and P. natalensis. There is to my knowledge no established methodology for dealing with behavioural data of this nature (but see below), and to avoid repetitive description I have grouped data where appropriate (e.g. according to sex and reproductive condition).

Frequencies of total interaction (i.e. agonistic, amicable and sexual interaction combined) were subjected to analysis of variance (F-test) using the Del Scott Rummage programme on a Univac 1100 computer. The prepared data were not normally distributed and the variances were not homogeneous, but the distributions were more or less normalized by log transformation after adding one to each value. Adding one to each value prior to transformation may be used to eliminate large numbers of zero values (as in my data) prior to AOV (Sokal & Rohlf 1969). In discussing AOV it is customary to use the term "interaction" in reference to statistical significance. However, interaction in this work refers to social behaviour, and to avoid confusion the term is placed in quotes (i.e. "interaction") when used in its AOV sense.

Data other than those referred to above were unsuitable for parametric statistical comparison, and non-parametric tests (section 2.5) were used whenever practicable. The distributions of frequencies of amicable interaction in the three species (sections 5.3.2.1C, 5.3.2.2C) were compared using χ^2 contingency analysis. χ^2 tests are insensitive to the effects of order when degrees of freedom are greater than one (Sokal & Rohlf 1969).

Table 24 : Part of the variable matrix resulting from the study of social organization of captive O. irroratus, R. pumilio and P. natalensis. For additional details, see text.

VARIABLES			
1. SPECIES	2. CASTE COMBINATIONS	3. REPLICATIONS	4. OBSERVATION PERIODS
O. irroratus	Scrotal male/Scrotal male	1	1 2 3 4 5
		2	1 2 3 4 5
		3	1 2 3 4 5
		4	1 2 3 4 5
	Scrotal male/Perforate female		
	etc.		

Order was critical to these comparisons, since interaction frequencies differed not only between species, but also between observation periods for a given species. Therefore, comparisons were generally made using 2 x 5 contingency tables (i.e. for two species at a time), generally for those pairs of species for which the distributions (i.e. curves) were obviously closest. X^2 could not be used to compare frequencies of agonistic and sexual interaction since the frequencies for given observation periods were generally too small (see Siegel 1956, p.110), and differences were tentatively ascertained by inspection. Differences between percentages of total interaction devoted to amicable behaviour were also ascertained by inspection.

5.3. Results

5.3.1. Field studies

Indices of association (section 5.2.1) were based on 121 captures of 65 O. irroratus and 143 captures of 94 R. pumilio at the Dargle grassland, and 150 captures of 150 P. natalensis at Darvill. A total of 246 P. natalensis were removal-trapped at Darvill (section 3.3.1), but only the first 150 captures were used here so as to avoid the possibility of bias in comparing indices of association for this species with those for the other two. This number (150) was not significantly greater than the 121 captures of O. irroratus (X^2 = 3.10; P>.05), although the difference approaches significance, and there was no statistical difference between the numbers of captures used here for all three species (X^2_2 = 3.32; P>.05).

Numbers of captures (total, associated and isolated; section 5.2.1) of six castes of each species (section 2.2) are listed in Table 25.

Table 25. Total (T), associated (A) and isolated (I) captures of O. irroratus, R. pumilio and P. natalensis used to calculate indices of association.

CASTES	O. irroratus			R. pumilio			P. natalensis		
	T	A	I	T	A	I	T	A	I
Scrotal males	30	23	7	31	17	14	11	11	0
Perforate females	30	27	3	18	18	0	13	13	0
Non-scrotal males	14	11	3	13	8	5	38	38	0
Imperforate females	10	5	5	16	9	7	35	35	0
Sub-adults	26	21	5	16	13	3	31	31	0
Juveniles	11	10	1	49	39	10	22	22	0

Indices of association for 21 caste combinations of each species (section 2.2) are given in Table 26.

Inter- and intraspecific analyses of data are provided in sections 5.3.1.1 and 5.3.1.2 respectively, in which the term "adult complex" refers to the 10 caste combinations also studied in encounters (section 2.2).

5.3.1.1. Interspecific analysis

Composite indices of association for the three species (all 21 caste combinations) were as follows: O. irroratus 99.9, R. pumilio 90.4, and P. natalensis 621.5. It is clear from these indices that the P. natalensis population was far more highly aggregated than were those of O. irroratus and R. pumilio. This is borne out by the significant difference between the three species in the distributions of individual caste combination indices (Table 26) (H_2 = 26.94; P<.001). However, there was no significant difference between the distributions of the O. irroratus and R. pumilio individual indices (U = 203; z = 0.44; P = .33), and at the population level these species appear to have been similarly dispersed.

To permit direct comparison with the findings of the captive study (section 5.3.2), composite indices of association were calculated for the adult complex of each species, as follows: O. irroratus 88.1, R. pumilio 53.6 and P. natalensis 336.9. The distribution of individual adult complex indices (Table 26) between the three species was significantly different (H_2 = 8.80; P<.05), with the P. natalensis values clearly higher than in the other two, between which there was no statistical difference (U = 40; P>.05). Hence, the adult complexes of each species appeared to have been dispersed in the same general way as the entire populations, with

Table 26. Indices of association of free-living O. irroratus, R. pumilio and P. natalensis.

CASTE COMBINATIONS	O. irroratus	R. pumilio	P. natalensis
Scrotal/scrotal	34.7	43.0	10.1
Scrotal/perforate	58.3	21.3	24.3
Scrotal/non-scrotal	10.1	4.9	66.0
Scrotal/imperforate	10.0	42.6	68.1
Perforate/perforate	32.6	0	32.9
Perforate/non-scrotal	27.8	0	52.5
Perforate/imperforate	4.2	0	36.5
Non-scrotal/non-scrotal	4.0	22.8	150.1
Non-scrotal/imperforate	16.7	69.0	131.9
Imperforate/imperforate	33.3	0	184.6
Sub-adult/scrotal	33.0	14.2	57.5
Sub-adult/perforate	37.8	0	30.3
Sub-adult/non-scrotal	4.7	15.3	206.1
Sub-adult/imperforate	2.3	5.2	141.9
Sub-adult/sub-adult	18.1	18.2	222.6
Sub-adult/juvenile	0	15.2	201.0
Juvenile/scrotal	0	4.7	53.9
Juvenile/perforate	21.7	26.3	25.2
Juvenile/non-scrotal	6.7	2.7	112.3
Juvenile/imperforate	7.9	13.5	86.4
Juvenile/juvenile	15.2	71.3	144.9

P. natalensis most highly aggregated and O. irroratus and R. pumilio less so. In spite of the absence of statistical significance in the distribution of individual indices between O. irroratus and R. pumilio, the difference in adult complex indices suggests O. irroratus to have been more cohesively dispersed than R. pumilio.

5.3.1.2. Intraspecific analysis

Composite indices of association according to sex and reproductive condition in the adult complexes of the three species are given in Table 27. The sample sizes were too small for effective statistical comparison of the distributions of the individual indices (Table 26), but numerical differences in the composite indices permit the tentative conclusions summarized in Table 27.

5.3.2. Captive studies

Descriptions of patterns of interaction in the 10 dyadic combinations of each species are given in Table 28.

Section 5.3.2.1 provides a comparative account of interaction in O. irroratus, R. pumilio and P. natalensis, dealing with species totals and means, and describing relative sociability at the whole species level. Variation within species is dealt with in section 5.3.2.2. In both sections consideration is given to total interaction and its sub-divisions: agonistic, amicable (including sexual; Happold 1973, 1976) and sexual behaviour. The same general format is used in both sections, with analyses in terms of numbers of interacting dyads and numbers of observation periods in which interaction occurred (A), time elapsed to first observed amicable

Table 27. Composite indices of association and summary of relative propensities for association according to sex and reproductive condition of free-living adult O. irroratus, R. pumilio and P. natalensis. "Greater than" (>) and "equal to" (=) refer to relative propensities for association according to the indices in this table. M = male; F = female; R = reproductive; N = non-reproductive.

SPECIES / COMBINATION	O. irroratus	R. pumilio	P. natalensis
SEX:			
Male/male	29.1	35.5	182.2
Female/female	34.4	0	173.8
Male/female	58.0	49.0	162.1
Summary	M/F>M/M=F/F	M/M=M/F>F/F	M/M=F/F=M/F
REPRODUCTIVE CONDITION:			
Reproductive/reproductive	86.7	47.8	45.9
Non-reproductive/ non-reproductive	24.6	22.1	289.5
Reproductive/non-reproductive	25.0	17.4	109.6
Summary	R/R>N/N=R/N	R/R>N/N=R/N	N/N>R/N>R/R

Table 28. Patterns of interaction in O. irroratus, R. pumilio and P. natalensis encounters. A = number of dyads in which at least partially amicable relationships developed; N = number of dyads in which nest-sharing was observed.

COMBINATIONS	O. irroratus		R. pumilio		P. natalensis	
	Interaction	A N	Interaction	A N	Interaction	A N
SPECIES CHARACTERISTICS	Aggression high intensity but apparently ritualized (section 4.4.2); heavier animal almost invariably more aggressive than lighter, irrespective of sex; interaction entirely agonistic on day one of encounters; intensity of aggression usually declining after day one.	19 10	Aggression high intensity and direct, and apparently unritualized (section 4.4.2); males invariably more aggressive than females, irrespective of mass.	38 17	Aggression relatively low intensity and apparently ritualized (section 4.4.2); males invariably more aggressive than females, irrespective of mass.	39 35
SCROTAL/SCROTAL	Tendency for mutual avoidance after day one.	1 1	Initial agonism replaced by totally amicable interaction in all dyads.	4 3	Initial agonism largely replaced by mutual avoidance in two dyads, and amicability in two.	3 2

Continued overleaf

Table 28. Continued.

COMBINATIONS	O. irroratus			R. pumilio			P. natalensis		
	Interaction	A	N	Interaction	A	N	Interaction	A	N
SCROTAL/PERFORATE	Agonism initiated by male, but with females at times obtaining higher scores due to defensive overreaction; tendency for females to avoid males after day one.	2	1	Generally high frequencies of amicable interaction throughout; male sexual interest generally of brief duration.	4	3	Agonistic, amicable and sexual interaction generally interspersed.	4	2
SCROTAL/NON-SCROTAL	Tendency for non-scrotal avoidance of scrotal males; ready submission by non-scrotal males preventing attack by aggressors.	2	1	Generally well developed avoidance by non-scrotal of scrotal males.	4	1	No agonistic interaction observed; generally high levels of amicable behaviour throughout.	4	4
SCROTAL/IMPERFORATE	Tendency for female avoidance of males, but with one dyad displaying strong affinity after day one, including nest-sharing from day two.	3	1	Initial (day one) agonism occurring largely as result of female aggressive responses to male sexual approaches; courtship prolonged relative to scrotal/ perforate encounters.	4	2	Generally high levels of amicable interaction following initial agonism.	4	4

Continued overleaf

Table 28. Continued.

COMBINATIONS	*O. irroratus*		*R. pumilio*		*P. natalensis*	
	Interaction	A N	Interaction	A N	Interaction	A N
PERFORATE/PERFORATE	Agonism maintained throughout, with lighter animals avoiding contact as far as possible.	0 0	Generally high levels of amicable interaction throughout.	4 3	One dyad largely avoiding contact, although totally amicable; remainder amicable following initial agonism.	4 3
PERFORATE/NON-SCROTAL	Either animal initiating agonism on day one, and even greatly outweighed males non-submissive; interaction largely male-initiated in two encounters, and female-initiated in remaining two.	3 2	Day one agonism resulting from female aggression in response to male courtship behaviour; generally high frequencies of amicable and sexual interaction throughout.	4 2	Generally high levels of amicable interaction following initial agonism.	4 4
PERFORATE/IMPERFORATE	Initial agonism followed by imperforate avoiding perforate females; however, three dyads developing fully amicable relationships toward end of encounters.	3 3	Tendency for imperforate to avoid perforate females in two encounters, but fully amicable relationships developing in remaining two.	4 1	Generally very high levels of amicable interaction following initial agonism.	4 4

Continued overleaf

Table 28. Continued.

COMBINATIONS	O. irroratus			R. pumilio			P. natalensis		
	Interaction	A	N	Interaction	A	N	Interaction	A	N
NON-SCROTAL/NON-SCROTAL	Strong tendency for mutual avoidance following initial hostility.	1	1	Tendency for mutual avoidance in all but one dyad.	2	0	No agonistic interaction observed; generally high interaction frequencies following mutual avoidance on day one.	4	4
NON-SCROTAL/IMPERFORATE	Strong tendency for mutual avoidance.	1	0	Agonistic, amicable and sexual interaction generally interspersed.	4	1	Generally high frequencies of amicable interaction following brief initial agonism.	4	4
IMPERFORATE/IMPERFORATE	Some amicability following initial agonism, but at low frequencies.	3	0	Agonistic and amicable interaction generally interspersed.	4	1	Amicability levels generally high following initial brief agonistic sequences.	4	4

interaction and nest-sharing (B), interaction frequencies (C) and synopses of the most important features of subsections A-C (D).

5.3.2.1. Interspecific analysis

A. Numbers of dyads and observation periods

Total numbers of dyads and observation periods (respectively out of 40 and 200 for each species) in which interaction occurred (total, agonistic, amicable and sexual interaction, and nest-sharing), and the number of females fertilized during encounters, were subjected to X^2 analysis (Table 29), and the results summarized in Table 30. O. irroratus is omitted from comparison of reproductive interaction since its failure to breed in captivity (section 4.3.5) is clearly aberrant.

B. Time to first amicable interaction and nest-sharing

Mean time elapsed to first amicable interaction and nest-sharing in those dyads which developed such relationships (subsection A, above) differed significantly among the three species, with the O. irroratus values significantly higher than those for R. pumilio and P. natalensis, between which there were no significant differences (Table 31).

C. Interaction frequencies

Frequences of total interaction in the three species displayed significant "interaction" (in the AOV sense; section 5.2.2) ($F_2 = 47.03$; $P<.0000$). This "interaction" is reflected in the species means for total interaction, given as 10-second intervals/dyad/observation period:

Table 29. Interspecific analysis (χ^2) of interaction in O. irroratus, R. pumilio and P. natalensis encounters, in terms of numbers of interacting dyads and observation periods in which interaction occurred. Degrees of freedom given in brackets; P given where values of χ^2 were less than the 5% level of significance.

PARAMETERS	INTERACTION			χ^2	P
	O. irroratus	R. pumilio	P. natalensis		
TOTAL INTERACTION					
Dyads	38	39	40	0.05 (2)	
Observation periods	120	148	161	6.14 (2)	<.05
AGONISTIC INTERACTION	120		161	5.98 (1)	<.05
Dyads	38	29	29	1.69 (2)	
Observation periods	97	54	38	29.56 (2)	<.001
AMICABLE INTERACTION	97	54		12.25 (1)	<.001
Dyads	19	38	39	7.94 (2)	<.05
	19	38		6.33 (1)	<.05
Observation periods	39	128	157	70.02 (2)	<.001
NEST-SHARING					
Dyads	10	17	35	16.09 (2)	<.001
		17	35	6.23 (1)	<.05
Observation periods	17	41	82	46.30 (2)	<.001
	17	41		9.93 (1)	<.01
		41	82	13.67 (1)	<.001
SEXUAL INTERACTION					
Dyads	-	15	4	6.37 (1)	<.05
Observation periods	-	36	12	12.00 (1)	<.001
CONCEPTION*					
Number of females	-	4	0	4.00 (1)	<.05

* Fertilization during encounters

Table 30. Summary of interspecific analysis of interaction in O. irroratus (O), R. pumilio (R) and P. natalensis (P) encounters, in terms of numbers of interacting dyads and observation periods in which interaction occurred. "Greater than" (>) and "equal to" (=) respectively refer to differences below and above the 5% level of statistical significance; empty cells indicate no significant differences.

PARAMETERS	INTERACTION	
	Dyads	Observation periods
Total interaction		P>O; O=R; R=P
Agonistic interaction		O>R=P
Amicable interaction	P=R>O	P=R>O
Nest-sharing	P>R=O	P>R>O
Sexual interaction	R>P	R>P
Conception (females)*	R>P	-

* Fertilization during encounters

Table 31. Mean time elapsed to first amicable interaction and nest-sharing in O. irroratus, R. pumilio and P. natalensis encounters, and interspecific analysis (H, U) of distributions of individual values from which means were calculated. P given where values of H and U were less than the 5% level of significance.

PARAMETERS	MEAN TIME ELAPSED (HOURS)			STATISTICS Relating to Distributions
	O. irroratus	R. pumilio	P. natalensis	
Amicable interaction	56.9	13.9	6.7	$H_2 = 50.39$; $P<.001$
	56.9	13.9		$U = 464$; $z = 1.74$; $P = .0409$
		13.9	6.7	$U = 792$; $z = 0.64$
Nest-sharing	76.8	42.2	40.3	$H_2 = 61.00$; $P<.001$
	76.8	42.2		$U = 48$; $P<.05$
		42.2	40.3	$U = 290.5$; $z = 0.04$

O. irroratus 19.7, R. pumilio 55.6 and P. natalensis 64.5.

Mean frequencies of agonistic and amicable interaction and mean percentages of total interaction devoted to amicable behaviour are plotted against time (observation periods) in Figure 16. There was a general gradation in agonistic interaction: O. irroratus > R. pumilio > P. natalensis, which was particularly marked during the first observation period. O. irroratus displayed significantly lower levels of amicable interaction than either R. pumilio ($\chi^2_4 = 37.60$; $P<.001$) or P. natalensis ($\chi^2_4 = 21.79$; $P<.001$). The R. pumilio and P. natalensis distributions also differed significantly ($\chi^2_4 = 37.60$; $P<.01$), with the P. natalensis values generally the higher, but the curves were statistically indistinguishable during the first three observation periods ($\chi^2_2 = 4.09$; $P<.05$). Percentages of amicable interaction were initially far higher in R. pumilio and P. natalensis than in O. irroratus, but the difference decreased with time as the majority of O. irroratus dyads either developed amicable relationships or avoided contact.

Mean frequencies of sexual interaction in R. pumilio and P. natalensis male/female encounters were calculated for the 16 male/female dyads of each species (Figure 17A). The R. pumilio curve was higher than that of P. natalensis. In addition, Figure 17A illustrates the tendency for sexual activity in R. pumilio to decrease with time, while in P. natalensis it remained approximately constant (section 4.3.5). The disparity in overall levels of sexual behaviour in these two species (Figure 17A) was largely the result of the majority of R. pumilio male/female dyads engaging in courtship, while in P. natalensis only scrotal/perforate dyads did so. R. pumilio scrotal males indiscriminately courted both perforate and imperforate females, and two members of each female caste were fertilized

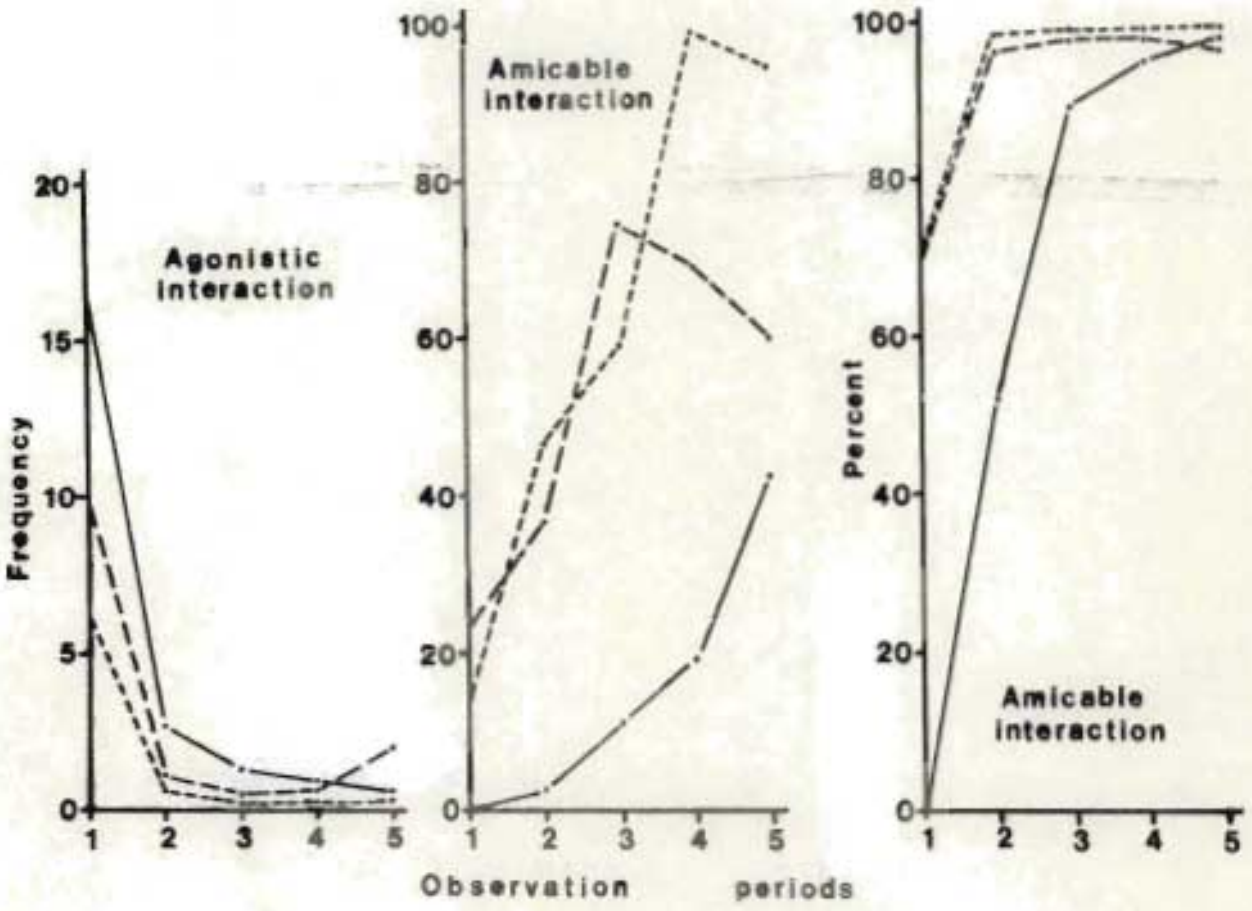

Figure 16. Mean frequencies of agonistic and amicable interaction, and percentages of amicable interaction in O. irroratus (——), R. pumilio (— —) and P. natalensis (----) encounters.

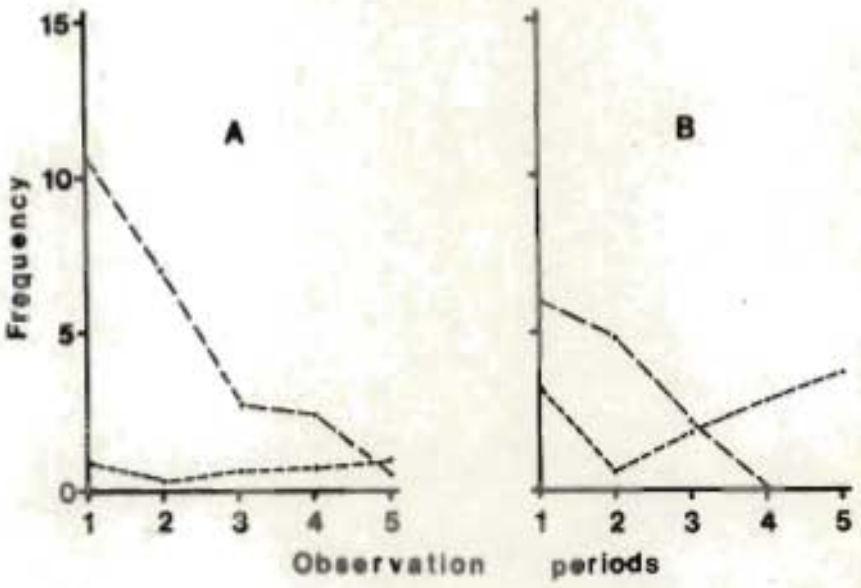

Figure 17. Mean frequencies of sexual interaction in R. pumilio (——) and P. natalensis (----) male/female (A) and scrotal male/perforate female (B) encounters.

by scrotal males during encounters. The apparent anomaly of sexually immature males engaging in precocial sexual activity may be explained in terms of rapid descent of the testes in males which were classified as non-scrotal at the start of encounters (section 2.2), but in which descent usually occurred before the third or fourth observation period. However, the testes never attained full size within the five-day period, and no females were fertilized by initially non-scrotal males.

Figure 17B shows the distribution of mean frequencies of sexual interaction in R. pumilio and P. natalensis scrotal/perforate dyads. The differing tendencies of the two species in respect of sexual activity in time (above) are well illustrated in this figure.

Interaction in relation to parturition and lactation was studied in two categories of R. pumilio and P. natalensis dyads, ones in which a scrotal male and pregnant female were combined a maximum of four days before birth of the young (newly combined dyads), and ones which had been caged together for at least one month before birth (established dyads). This study was qualitative, but is reported here rather than in section 4 since the length of time dyads had been caged together directly influenced survival of the young, and hence bears directly on social organization. Interaction in newly combined and established R. pumilio and P. natalensis dyads is described in Table 32. A single newly combined O. irroratus dyad was studied following introduction of a scrotal male to an encounter cage in which a female had produced two young five days previously. The male was intensely aggressive toward both female and young during the first (4h) observation period, and by the following day the young had been killed, presumably by the male. The male itself had been badly injured on the face and neck, presumably by the female, and the animals were separated.

Table 32. Interaction in relation to parturition and lactation in R. pumilio and P. natalensis established and newly combined dyads. For definitions of "established" and "newly combined", see text.

FUNCTIONAL UNITS	COMMON TO BOTH SPECIES	R. pumilio		P. natalensis	
		Established	Newly combined	Established	Newly combined
PARTURITION	ESTABLISHED DYADS: Male and female nesting together prior to birth of young; parturition not observed.	Nest-building activity of female increasing at least one day before parturition; Brooks (1974) notes male being present during parturition, at times grooming female and young.		No increase in nest-building activity; female evicting all other animals from nest before parturition (Cilliers 1972).	
	NEWLY COMBINED DYADS: Pregnant female always attempting to preclude male from her nest; parturition not observed, but male almost certainly precluded; young always abandoned or killed, usually within few hours of birth; adults largely amicable after parturition, but female always attempting to preclude male from her nest while young alive.		Dyads often intensely agonistic before parturition, with either animal initiating aggression; female tending to hyperactivity, attempting to escape from cage.		Female initiating aggression; male rarely aggressive, but female repulsing all approaches by male; Cilliers (1972) notes that pregnant female may chase males which are some distance from her nest; male once observed removing young from nest but not killing them; stressed females may kill their own young (Choate 1972; Cilliers 1972).

Continued overleaf

Table 32. Continued.

FUNCTIONAL UNITS	COMMON TO BOTH SPECIES	*R. pumilio*		*P. natalensis*	
		Established	Newly combined	Established	Newly combined
LACTATION	ESTABLISHED DYADS ONLY: Total amicability, with male usually sharing nest with female and young; post-partum oestrus usual.	Male excluded from nest in some cases (Choate 1972; Marais 1972).		Other females, but not males, permitted to enter nest (Cilliers 1972), with lactating females tolerating only companions of long standing (Choate 1972).	

The first two litters born to an established R. pumilio dyad normally survived, forming a group of 10-12 animals in most cases, but a third litter did not survive, and thereafter breeding was curtailed while the group was maintained together. Even in a holding cage interaction in such a group was entirely amicable until onset of sexual maturity in members of the first litter, when the group had to be separated to prevent mortality of animals apparently competing for breeding rights. In P. natalensis survival of two or three litters comprising up to 25 young was usual before sustained anoestrus in the female, as noted by Choate (1972). Such groups were too large to be maintained together once the young approached adult size, and the first litter was generally removed at about six weeks old, when sexual maturity was imminent (Baker & Meester 1977). Housing an entire P. natalensis litter in a holding cage often resulted in all of the animals (males and females) surviving to sexual maturity and commencement of reproductive activity.

The relationship between parturition and sexual activity in established R. pumilio and P. natalensis dyads, each comprising a scrotal male and pregnant female, was quantitatively studied in four dyads/species (Figure 18). This figure, which illustrates mean frequencies of sexual interaction, shows that sexual activity in R. pumilio was strictly post-partum, but while P. natalensis displayed a sexual peak immediately following parturition, sexual contact was maintained before as well as after the assumed post-partum oestrus.

D. Synopsis

The evidence presented above (subsections A-C) shows unequivocally that under the conditions of the present study O. irroratus displays a far

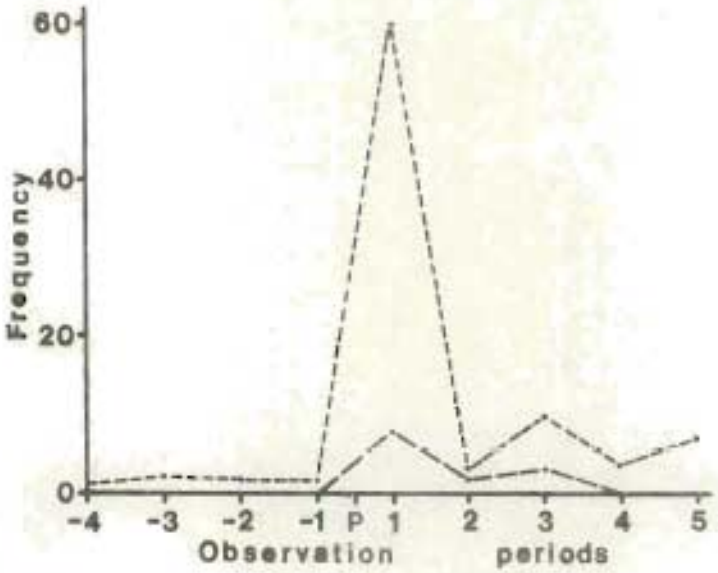

Figure 18. Mean frequencies of sexual interaction in R. pumilio (——) and P. natalensis (----) scrotal male/perforate female encounters in relation to parturition (P).

lower propensity for interaction and development of amicable relationships than either R. pumilio or P. natalensis. Overall levels of interaction and amicability were generally similar in R. pumilio and P. natalensis, although P. natalensis scores for these parameters were in all respects higher than in R. pumilio. In particular, the high number of P. natalensis dyads in which nest-sharing occurred appears to place this species above R. pumilio on an ascending scale of relative sociability.

During the first observation period O. irroratus dyads were consistently hostile at interaction frequencies that were higher than those of periods 2 and 3, during which animals tended to avoid contact. However, overall interaction levels rose during the later stages of encounters as a relatively small proportion of dyads developed fully amicable, nest-sharing relationships. Once such relationships had developed in O. irroratus they were more or less stable, as evidenced by the increase towards the end of the five-day period in mean frequencies of amicable interaction, and steadily declining agonism. In contrast, amicability predominated from the outset in R. pumilio and P. natalensis, and interaction frequencies were higher than in O. irroratus for given observation periods. However, in both R. pumilio and P. natalensis mean frequencies of amicable interaction declined toward the end of the five-day period. In P. natalensis the decline was small enough to be disregarded, but in R. pumilio it appeared to represent a definite trend. This conclusion is reinforced by the increase in agonistic interaction in R. pumilio during the fifth period.

A higher proportion of total interaction was devoted to sexual activity by R. pumilio than by P. natalensis. Additional phenomena associated with sexual behaviour in R. pumilio were the tendency for sexual activity to decline with time, the involvement of males in courtship prior to full sexual maturity, and the relatively high rate of fertilization which

occurred during encounters. These traits were lacking in P. natalensis.

5.3.2.2. Intraspecific analysis

Interaction in the 40 encounters for each species was analysed in terms of arrangements of data according to the sex and reproductive condition of dyadic partners, as follows (numbers of dyads in brackets):

SEX: male/male (12); female/female (12); male/female (16);

REPRODUCTIVE CONDITION: reproductive/reproductive (12); non-reproductive/non-reproductive (12); reproductive/non-reproductive (16).

Reference should be made to Table 28 for details of interaction in individual dyadic combinations.

A. Numbers of dyads and observation periods

Prior to analysis, data for male/female and reproductive/non-reproductive encounters were corrected (by multiplying by 0.75) to reflect values comparable with those for the remaining combinations (i.e. scores out of 12 and 60 for numbers of dyads and observation periods respectively). Total numbers of dyads and observation periods in which interaction occurred (total, agonistic and amicable interaction, and nest-sharing) were compared using χ^2 analysis in Tables 33 (data arranged according to the sex of dyadic partners) and 34 (reproductive condition), and the results summarized in Table 35.

B. Time to first amicable interaction and nest-sharing

Mean time elapsed to first amicable interaction and nest-sharing in

Table 33 : Intraspecific analysis (X^2) of interaction in O. irroratus, R. pumilio and P. natalensis encounters according to the sex of dyadic partners, in terms of numbers of interacting dyads and observation periods in which interaction occurred. M = male; F = female; degrees of freedom given in brackets; P given where values of X^2 were less than the 5% level of significance.

PARAMETERS	INTERACTION			X^2	P
	M/M	F/F	M/F		
O. irroratus					
TOTAL INTERACTION					
Dyads	11	12	11.2	0.05 (2)	
Observation periods	32	41	35.2	1.15 (2)	
AGONISTIC INTERACTION					
Dyads	11	12	11.2	0.05 (2)	
Observation periods	28	32	27.7	0.39 (2)	
AMICABLE INTERACTION					
Dyads	4	6	6.7	0.70 (2)	
Observation periods	8	12	14.2	1.73 (2)	
NEST-SHARING					
Dyads	3	3	3	0.00 (2)	
Observation periods	4	4	6.7	0.99 (2)	
R. pumilio					
TOTAL INTERACTION					
Dyads	10	12	12	0.24 (2)	
Observation periods	37	46	48.7	1.71 (2)	
AGONISTIC INTERACTION					
Dyads	10	9	7.5	0.36 (2)	
Observation periods	22	16	12	3.03 (2)	
AMICABLE INTERACTION					
Dyads	10	12	12	0.24 (2)	
Observation periods	24	42	46.5	7.56 (2)	<.05
	24	42		4.91 (1)	<.05

Table 33. Continued.

PARAMETERS	INTERACTION			χ^2	P
	M/M	F/F	M/F		
NEST-SHARING					
Dyads	4	5	6	0.40 (2)	
Observation periods	8	17	12	3.31 (2)	
P. natalensis					
TOTAL INTERACTION					
Dyads	12	12	12	0.00 (2)	
Observation periods	40	53	51	2.04 (2)	
AGONISTIC INTERACTION					
Dyads	4	11	10.5	3.59 (2)	
Observation periods	6	13	14.2	3.54 (2)	
AMICABLE INTERACTION					
Dyads	11	12	12	0.06 (2)	
Observation periods	38	52	50.2	2.48 (2)	
NEST-SHARING					
Dyads	10	11	10.5	0.05 (2)	
Observation periods	22	23	27.7	0.77 (2)	

Table 34. Intraspecific analysis (χ^2) of interaction in O. irroratus, R. pumilio and P. natalensis encounters according to the reproductive condition of dyadic partners, in terms of numbers of interacting dyads and observation periods in which interaction occurred. R = reproductive; N = non-reproductive; degrees of freedom given in brackets; P given where values of χ^2 were less than the 5% level of significance.

PARAMETERS	INTERACTION			χ^2	P
	R/R	N/N	R/N		
O. irroratus					
TOTAL INTERACTION					
Dyads	12	11	11.2	0.05 (2)	
Observation periods	40	26	40.5	3.82 (2)	
AGONISTIC INTERACTION					
Dyads	12	11	11.2	0.05 (2)	
Observation periods	38	20	29.2	5.57 (2)	
AMICABLE INTERACTION	38	20		5.59 (1)	<.05
Dyads	3	5	8.2	2.76 (2)	
Observation periods	6	8	18.7	8.56 (2)	<.05
		8	18.7	4.29 (1)	<.05
NEST-SHARING					
Dyads	2	1	5.2	3.57 (2)	
Observation periods	2	1	10.5	12.11 (2)	<.01
	2		10.5	5.78 (1)	<.05
R. pumilio					
TOTAL INTERACTION					
Dyads	12	10	12	0.24 (2)	
Observation periods	50	40	43.5	1.16 (2)	
AGONISTIC INTERACTION					
Dyads	7	10	9	0.54 (2)	
Observation periods	10	23	15.7	5.24 (2)	
AMICABLE INTERACTION	10	23		5.12 (1)	<.05
Dyads	12	10	12	0.24 (2)	
Observation periods	46	33	36.7	2.36 (2)	

Continued overleaf

Table 34. Continued.

PARAMETERS	INTERACTION			X^2	P
	R/R	N/N	R/N		
NEST-SHARING					
Dyads	9	2	4.5	4.84 (2)	
	9	2		4.45 (1)	<.05
Observation periods	28	2	8.2	29.04 (2)	<.001
	28		8.2	10.83 (1)	<.001
P. natalensis					
TOTAL INTERACTION					
Dyads	12	12	12	0.00 (2)	
Observation periods	44	47	52.5	0.78 (2)	
AGONISTIC INTERACTION					
Dyads	11	7	8.2	0.97 (2)	
Observation periods	19	7	8.2	7.66 (2)	<.05
	19		8.2	4.29 (1)	<.05
AMICABLE INTERACTION					
Dyads	11	12	12	0.06 (2)	
Observation periods	41	47	51.7	1.23 (2)	
NEST-SHARING					
Dyads	7	12	12	1.62 (2)	
Observation periods	10	27	33.7	12.65 (2)	<.01
	10	27		7.81 (1)	<.01

Table 35 : Summary of intraspecific analysis of interaction in O. irroratus, R. pumilio and P. natalensis encounters according to the sex and reproductive condition of dyadic partners, in terms of numbers of interacting dyads and observation periods in which interaction occurred. "Greater than" (>) and "equal to" (=) respectively refer to differences below and above the 5% level of statistical significance; empty cells indicate no significant differences; M = male; F = female; R = reproductive; N = non-reproductive.

PARAMETERS	SEX		REPRODUCTIVE CONDITION	
	Dyads	Observation Periods	Dyads	Observation Periods
O. irroratus				
Total interaction				
Agonistic interaction				R/R>N/N; R/R=R/N; N/N=R/N
Amicable interaction				R/N>R/R=N/N
Nest-sharing				R/N>R/R=N/N
R. pumilio				
Total interaction				
Agonistic interaction				N/N>R/R; R/R=R/N; N/N=R/N
Amicable interaction		F/F=M/F>M/M		
Nest-sharing			R/R>N/N; R/R=R/N; N/N=R/N	R/R>R/N=N/N
P natalensis				
Total interaction				
Agonistic interaction				R/R>R/N=N/N
Amicable interaction				
Nest-sharing				N/N=R/N>R/R

those O. irroratus and R. pumilio dyads in which such behaviour was observed did not differ significantly according to either the sex (Table 36) or reproductive condition of dyadic partners (Table 37). P. natalensis male/male dyads took significantly longer than either of the other two combinations (female/female, male/female) to make amicable contact (Table 36); nest-sharing first occurred significantly later in reproductive/reproductive dyads of this species than in non-reproductive/non-reproductive and reproductive/non-reproductive ones (Table 37).

C. Interaction frequencies

Mean frequencies of total interaction according to the sex and reproductive condition of dyadic partners are illustrated for the three species in Figure 19. Results of X^2 analysis of the values on which Figure 19 are based are given in Table 38.

Mean daily frequencies of agonistic and amicable interaction, and percentages of amicable behaviour are illustrated according to sex and reproductive condition in Figures 20 (O. irroratus), 21 (R. pumilio) and 22 (P. natalensis). In the cases of R. pumilio and P. natalensis, comparison of the curves in these figures was carried out as in section 5.3.2.1C (Table 39), but this was impossible for O. irroratus (see section 5.2.2), and all differences in respect of sex and reproductive condition in this species were tentatively ascertained by inspection. Similarly, in some cases contingency analysis showed pairs of curves (Figures 21, 22) to be significantly different (Table 39), but day to day variability in levels of amicable interaction made it necessary to ascertain by inspection which curve was generally the higher.

Table 36. Mean time elapsed to first amicable interaction and nest-sharing in O. irroratus, R. pumilio and P. natalensis encounters according to the sex of dyadic partners, and intraspecific analysis (H, U) of distributions of individual values from which means were calculated. M = male; F = female; P given where values of H and U were less than the 5% level of significance.

PARAMETERS	MEAN TIME ELAPSED (HOURS)			STATISTICS Relating to Distributions
	M/M	F/F	M/F	
O. irroratus				
Amicable interaction	65.7	59.4	51.3	$H_2 = 1.14$
Nest-sharing	87.5	87.6	60.7	$H_2 = 2.60$
R. pumilio				
Amicable interaction	21.2	15.6	8.1	$H_2 = 1.04$
Nest-sharing	60.4	33.7	38.4	$H_2 = 2.66$
P. natalensis				
Amicable interaction	15.4	2.9	3.6	$H_2 = 10.38$; $P<.01$
	15.4		3.6	$U = 32$; $P<.01$
Nest-sharing	38.7	45.8	37.1	$H_2 = 0.39$

Table 37. Mean time elapsed to first amicable interaction and nest-sharing in O. irroratus, R. pumilio and P. natalensis encounters according to the reproductive condition of dyadic partners, and intraspecific analysis (H, U) of distributions of individual values from which means were calculated. R = reproductive; N = non-reproductive; P given where values of H and U were less than the 5% level of significance.

PARAMETERS	MEAN TIME ELAPSED (HOURS)			STATISTICS Relating to Distributions
	R/R	N/N	R/N	
O. irroratus				
Amicable interaction	36.0	61.9	60.3	$H_2 = 3.88$
Nest-sharing	96.0	96.0	68.6	$H_2 = 3.42$
R. pumilio				
Amicable interaction	12.2	17.1	13.2	$H_2 = 3.30$
Nest-sharing	33.3	60.3	49.9	$H_2 = 2.81$
P. natalensis				
Amicable interaction	4.4	9.9	5.9	$H_2 = 1.98$
Nest-sharing	72.0	34.3	30.9	$H_2 = 11.31$; $P<.01$
	72.0	34.3		$U = 20$; $P<.05$
		34.3	30.9	$U = 94.5$

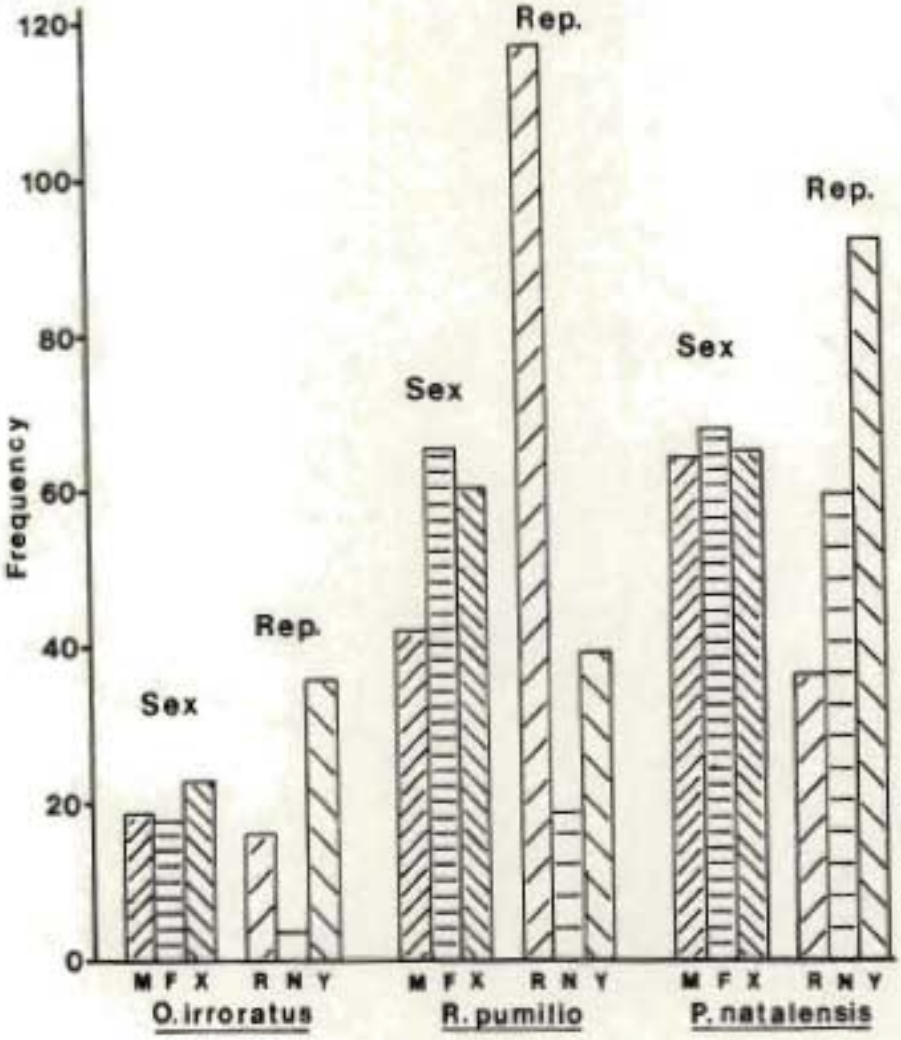

Figure 19. Mean frequencies of total interaction in O. irroratus, R. pumilio and P. natalensis encounters according to the sex and reproductive condition (Rep.) of dyadic partners. M = male/male; F = female/female; X = male/female; R = reproductive/reproductive; N = non-reproductive/non-reproductive; Y = reproductive/non-reproductive.

Table 38. Intraspecific analysis (X^2) of interaction in O. irroratus, R. pumilio and P. natalensis encounters according to the sex and reproductive condition of dyadic partners, in terms of mean frequencies of total interaction. M = male; F = female; R = reproductive; N = non-reproductive; degrees of freedom given in brackets; P given where values of X^2 were less than the 5% level of significance.

SPECIES	SEX			REPRODUCTIVE CONDITION		
	Test	X^2	P	Test	X^2	P
O. irroratus	M/M, F/F, M/F	0.69 (2)		R/R, N/N, R/N	28.58 (2)	<.001
				R/R, N/N	7.16 (1)	<.01
				R/R, R/N	4.00 (1)	<.05
R. pumilio	M/M, F/F, M/F	5.26 (2)		R/R, N/N, R/N	90.21 (2)	<.001
	M/M, F/F	5.01 (2)	<.05	R/R, R/N	37.95 (1)	<.001
	M/M, M/F	3.04 (1)		N/N, R/N	7.05 (1)	<.01
P. natalensis	M/M, F/F, M/F	0.11 (2)		R/R, N/N, R/N	25.18 (2)	<.001
				R/R, N/N	5.54 (1)	<.05
				N/N, R/N	7.12 (1)	<.01

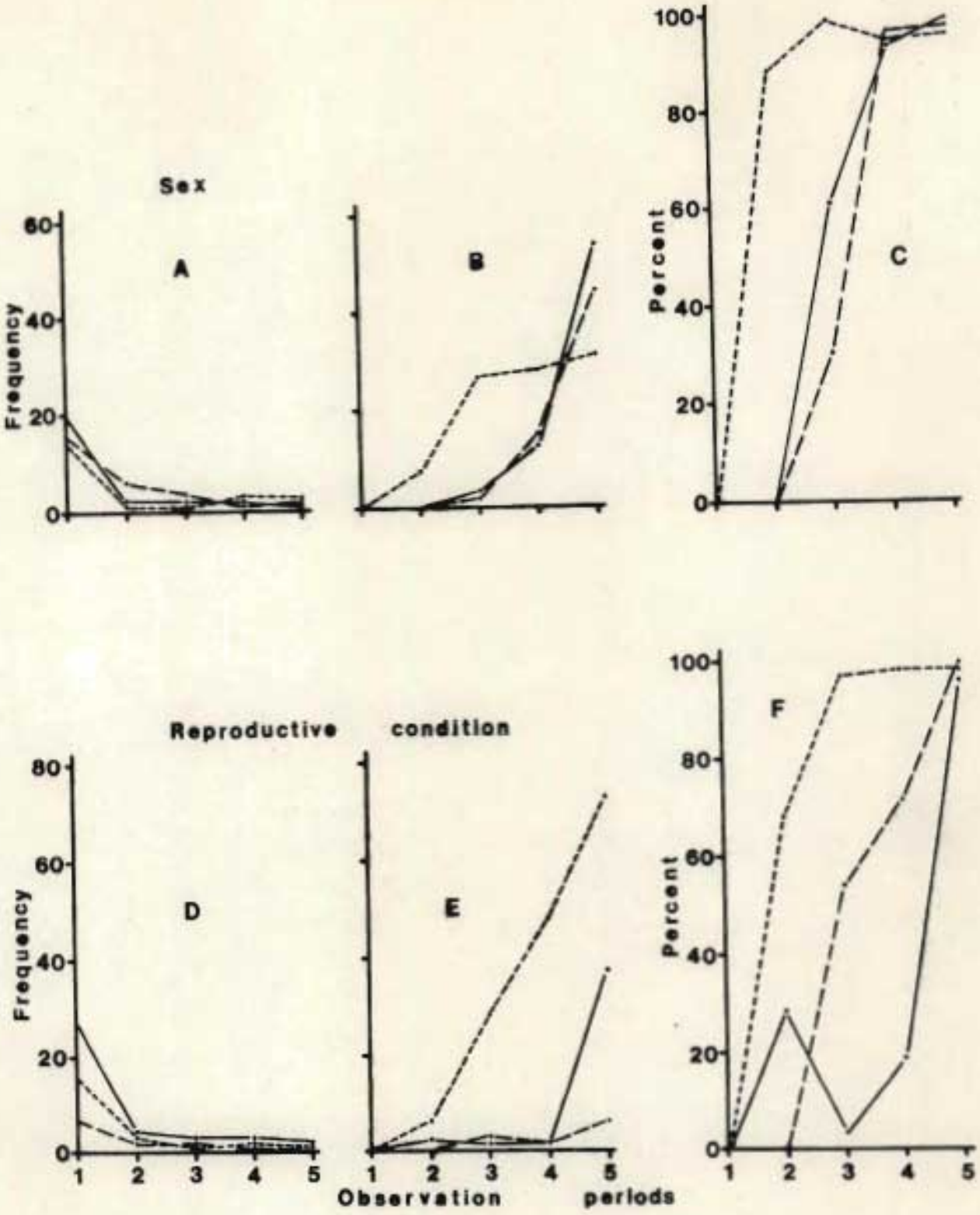

Figure 20. Mean frequencies of agonistic (A, D) and amicable interaction (B, E), and percentages of amicable interaction (C, F) in O. irroratus encounters according to the sex (A, B, C) and reproductive condition (D, E, F) of dyadic partners. Curves: sex - male/male ——; female/female —–; male/female ----; reproductive condition - reproductive/reproductive ——; non-reproductive/non-reproductive — —; reproductive/non-reproductive —·—.

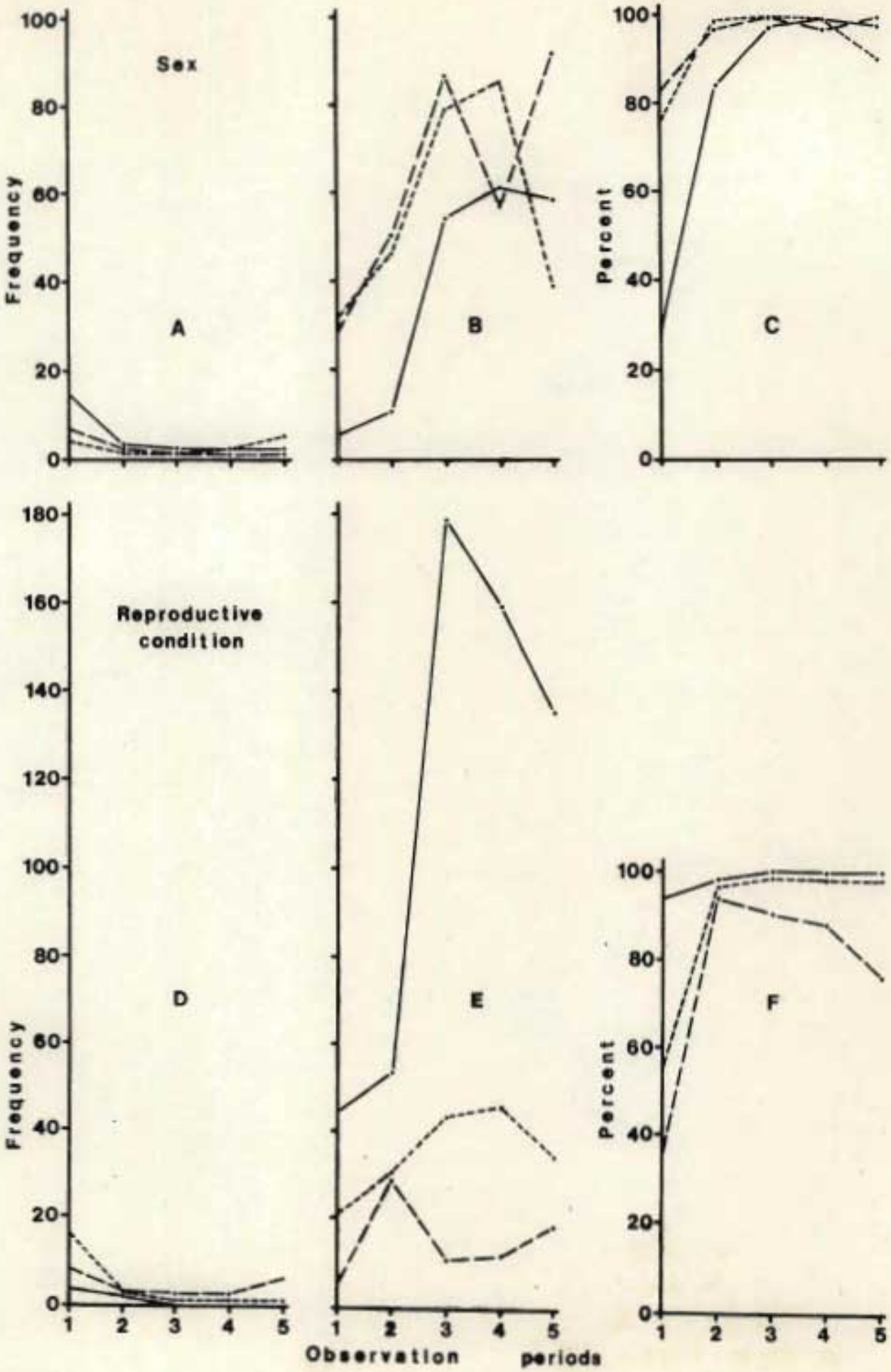

Figure 21. R. pumilio. Legend as for Figure 20.

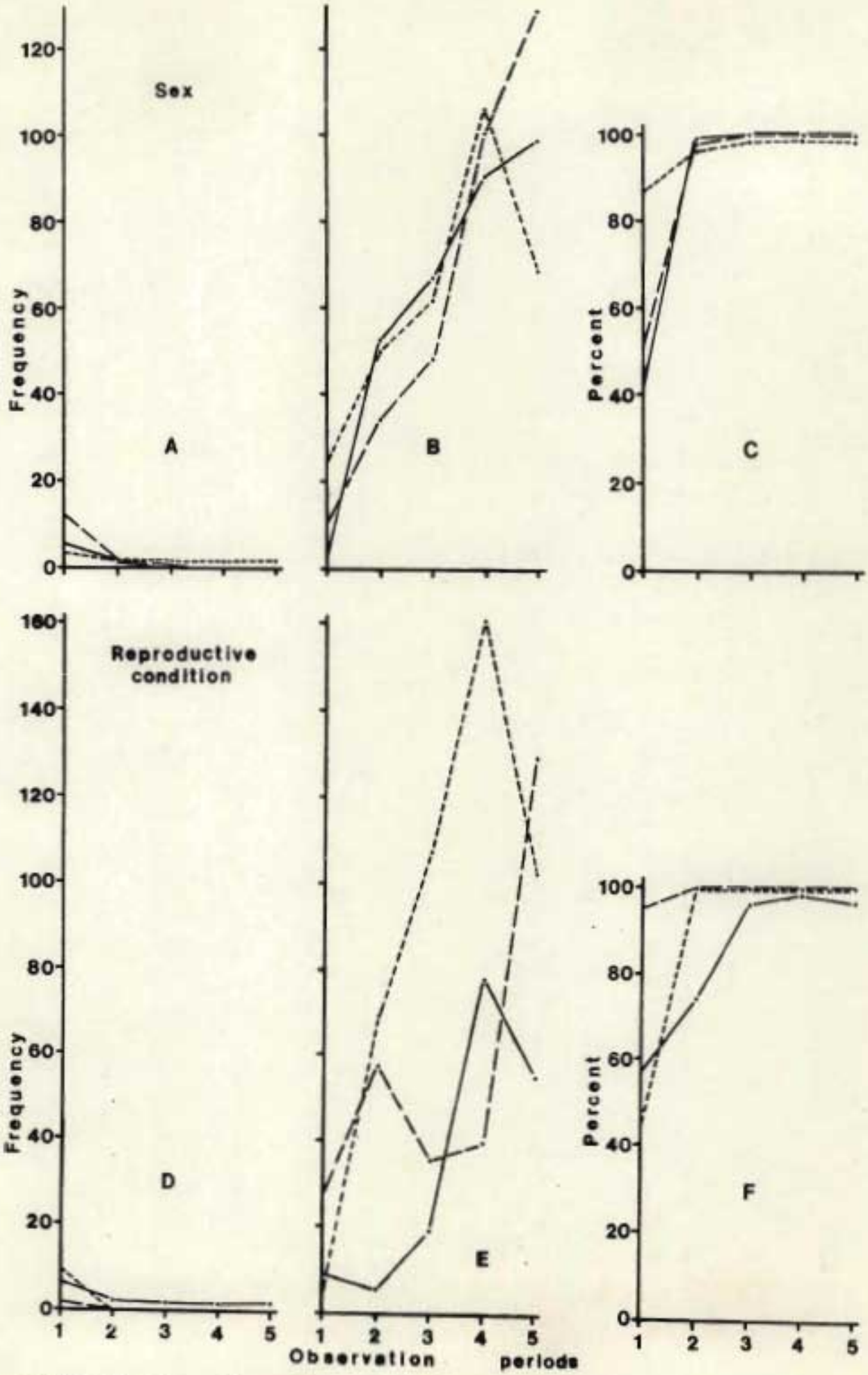

Figure 22. P. natalensis. Legend as for Figure 20.

Table 39. Intraspecific analysis (X^2) of interaction in R. pumilio and P. natalensis encounters according to the sex and reproductive condition of dyadic partners, in terms of mean frequencies of amicable interaction. M = male; F = female; R = reproductive; N = non-reproductive; degrees of freedom given in brackets; P given where values of X^2 were less than the 5% level of significance.

SPECIES	SEX			REPRODUCTIVE CONDITION		
	Test	X^2	P	Test	X^2	P
R. pumilio	M/M, F/F	28.84 (4)	<.001	R/R, N/N	54.90 (4)	<.001
	M/M, M/F	37.98 (4)	<.001	R/R, R/N	14.51 (4)	<.01
	F/F, M/F	26.22 (4)	<.001	N/N, R/N	17.37 (4)	<.01
P. natalensis	M/M, F/F	16.58 (4)	<.01	R/R, N/N	72.09 (4)	<.001
	M/M, M/F	25.75 (4)	<.001	R/R, R/N	38.01 (4)	<.001
	F/F, M/F	31.73 (4)	<.001	N/N, R/N	99.46 (4)	<.001

Table 40 provides a summary of intraspecific differences according to sex and reproductive condition, in terms of the parameters referred to above.

Only in R. pumilio did sexual interaction occur in more than one male/female dyadic combination (section 5.3.2.1), and totals of mean daily frequencies were as follows: scrotal/perforate 12.8; scrotal/imperforate 31.5; non-scrotal/perforate 31.5; non-scrotal/imperforate 13.0. These values are significantly different ($\chi^2_3 = 18.30$; $P<.001$). In addition, frequencies of sexual interaction in dyads in which the animals were in the same reproductive condition (i.e. scrotal/perforate; non-scrotal/imperforate) were significantly lower ($\bar{X} = 12.9$) than in reproductive/non-reproductive dyads ($\bar{X} = 33.3$) ($\chi^2 = 9.01$; $P<.01$).

D. Synopsis

The scores for nine of the 14 parameters analysed above (subsections A, B, C) were significantly different according to either or both sex and reproductive condition for one or more of the three species (Table 41). In the foregoing, "greater than" (>) indicated lower rather than higher amicability when referred to three parameters (numbers of observation periods during which agonistic interaction occurred, and mean time elapsed to first observed amicable interaction and nest-sharing). This inequality has been corrected in Table 41, and > infers higher amicability in all cases.

The information contained in Table 41 has been condensed for the two arrangements of data (sex and reproductive condition) for each species by totalling numerical values allocated for each parameter, as follows:

Table 40. Summary of intraspecific analysis of interaction in O. irroratus, R. pumilio and P. natalensis encounters according to the sex and reproductive condition of dyadic partners, in terms of mean frequencies of total, agonistic and amicable interaction, and percentages of amicable interaction. "Greater than" (>) and "equal to" (=) respectively refer to differences below and above the 5% level of statistical significance, or as distinguished by inspection; empty cells indicate no significant differences; M = male; F = female; R = reproductive; N = non-reproductive.

PARAMETERS	SUMMARY OF INTERACTION	
	Sex	Reproductive Condition
O. irroratus		
Total interaction		R/N>R/R>N/N
Agonistic interaction		R/R>N/N>R/N
Amicable interaction	M/F>M/M=F/F	R/N>R/R>N/N
% amicable interaction	M/F>M/M=F/F	R/N>R/R=N/N
R. pumilio		
Total interaction	F/F>M/M; M/M=M/F; F/F=M/F	R/R>R/N>N/N
Agonistic interaction		N/N=R/N>R/R
Amicable interaction	F/F=M/F>M/M	R/R>R/N>N/N
% amicable interaction	F/F=M/F>M/M	R/R>R/N>N/N
P. natalensis		
Total interaction		R/N>N/N>R/R
Agonistic interaction		
Amicable interaction		N/N=R/N>R/R
% amicable interaction		N/N>R/N>R/R

Table 41. Relative amicability according to the sex and reproductive condition of dyadic partners in O. irroratus, R. pumilio and P. natalensis encounters, in terms of nine parameters of sociability, summarized from subsections A, B and C (above). "Greater than" (>) and "equal to" (=) respectively refer to differences below and above the 5% level of statistical significance, or as distinguished by inspection; empty cells indicate no significant differences; M = male; F = female; R = reproductive; N = non-reproductive.

PARAMETERS	O. irroratus		R. pumilio		P. natalensis	
	Sex	Reproductive condition	Sex	Reproductive condition	Sex	Reproductive condition
A. NUMBERS						
Agonistic interaction		N/N>R/R		R/R>N/N		N/N=R/N>R/R
Amicable interaction		R/N>R/R=N/N	F/F=M/F>M/M			
Nest-sharing (periods)		R/N>R/R=N/N		R/R>R/N=N/N		N/N=R/N>R/R
Nest-sharing (dyads)				R/R>N/N		
B. TIME						
Amicable interaction					F/F=M/F>M/M	
Nest-sharing						N/N=R/N>R/R
C. FREQUENCIES						
Total interaction		R/N>R/R>N/N	F/F>M/M	R/R>R/N>N/N		R/N>N/N>R/R
Amicable interaction	M/F>M/M=F/F	R/N>R/R>N/N	F/F=M/F>M/M	R/R>R/N>N/N		N/N=R/N>R/R
% amicable interaction	M/F>M/M=F/F	R/N>R/R=N/N	F/F=M/F>M/M	R/R>R/N>N/N		N/N>R/N>R/R

a score of two in cases where the values of two combinations were significantly lower than that of the one under consideration, and a score of one where only a single value was lower. For example, in a hypothetical case A > B > C, A would score two, B one, and C zero. The total scores allocated in this way, together with the resulting summaries, are given in Table 42.

5.4. Discussion

The field studies (section 5.3.1) set out to confirm and enlarge on the findings of earlier reports on O. irroratus (Davis 1973), R. pumilio (Brooks 1974; Marais 1974) and P. natalensis (Coetzee 1967; Cilliers 1972; De Wit 1972), and to provide standardized data capable of direct comparison. In addition, the captive studies (section 5.3.2) were relatively comprehensive. Whereas trapping records give a basic understanding of social organization in free-living societies, captive studies may be of more use in elucidating the forces operating to maintain specific modes of dispersion (Eisenberg 1967). As a result of emphasizing the observational study using four castes, and analysing field data to consider six, the results suggest that the modes of dispersion of the three species comprise complexes of sub-systems in which the relative weighting of components (e.g. attraction, repulsion) is largely dependent on caste, sex and reproductive condition. It follows that complexes of social mechanisms underlie these sub-systems.

5.4.1. Relative sociability of O. irroratus, R. pumilio and P. natalensis

The captive study findings (section 5.3.2) supported by those in the field (section 5.3.1) showed P. natalensis to be generally more highly sociable than either O. irroratus or R. pumilio. However, while captive

Table 42. Relative amicability according to the sex and reproductive condition of dyadic partners in O. irroratus, R. pumilio and P. natalensis encounters, summarized from Table 41. See text for method of allocating scores. "Greater than" (>) and "equal to" (=) refer to relative amicability according to the scores in this table. M = male; F = female; R = reproductive; N = non-reproductive.

SPECIES	SEX			REPRODUCTIVE CONDITION		
	M/M	F/F	M/F	R/R	N/N	R/N
O. irroratus						
Total scores	0	0	4	2	1	10
Relative amicability	M/F>M/M=F/F			R/N>R/R>N/N		
R. pumilio						
Total scores	0	4	3	10	0	3
Relative amicability	F/F>M/F>M/M			R/R>R/N>N/N		
P. natalensis						
Total scores	0	1	1	0	7	7
Relative amicability	F/F=M/F>M/M			N/N=R/N>R/R		

R. pumilio were significantly more sociable than O. irroratus this did not appear to be the case in free-living populations, and R. pumilio was marginally the more dispersed of the two species. This ambiguity may be explained in terms of the following:

1. The social organization of O. irroratus appears to involve temporal territoriality (Davis 1973), and evidence is presented here which substantiates this conclusion (see section 5.4.2.1). The mechanism of temporal territoriality allows the home ranges of aggressive animals such as domestic cats to overlap in space but not in time, so that overlapping areas are utilised by different animals at different times, and by keeping strict "time schedules" (Leyhausen 1965, p.252) they generally avoid meeting face to face. Such a mechanism would permit the generally asocial and potentially highly aggressive O. irroratus (sections 4.3.3, 5.3.2) to exist in societies which are superficially relatively cohesive (section 5.3.1) but in which confrontation is avoided by the expedient of animals seldom meeting. Moreover, hierarchical ranking (Davis 1973; section 5.4.2.1) and ritualized aggression in this species (section 4.4.2) would permit de facto as well as trap-revealed close association between some members of O. irroratus societies. Leyhausen (1965) noted that while a kind of ranking order may exist in domestic cats it does not develop into a rigid hierarchical system. Such a system would be expected to obtain in O. irroratus.

2. R. pumilio societies, and breeding females in particular, are relatively highly dispersed during the breeding season (spring-autumn; see section 7.2.3), but tend to aggregate during the winter non-breeding period (Brooks 1974). Of the captures on which R. pumilio indices of association were based (section 5.3.1) over 90% were made

during the period October-April (section 3.3.1) when forces of repulsion within the population were probably at their highest (territoriality in lactating and/or pregnant females; competition for mating opportunities in reproductive males; section 5.4.2.2). This would account for the relatively low overall association in the free-living population. These mechanisms did not operate in encounters (section 5.3.2), and in the six intrasexual caste combinations reproductive activity was impossible. It is likely, therefore, that except in male/female encounters the levels of amicable interaction observed in captivity approximated those of reproductively quiescent rather than active R. pumilio.

5.4.2. Social organization

In discussing the social systems of the three species (sections 5.4.2.1, 5.4.2.2, 5.4.2.3) only those associations (section 5.3.1) and relationships (section 5.3.2) have been included that appeared most pertinent to the phenomena under consideration. Discussion is at an intraspecific level, and relative terms (e.g. high; low) refer to results for individual species, not to the combined spectrum for all three.

5.4.2.1. O. irroratus

A. Dispersion

On the basis of a high degree of intrasexual home range overlap a probably hierarchical social system was postulated for O. irroratus by Davis (1973) who, in addition, suggested the occurrence of intrasexual territorial defence in the vicinity of the nest. He also reported

extensive territorial overlap, leading to the suggestion that temporal territoriality might be represented in the social system of this species.

Development of at least partially amicable relationships in 19 encounters, with nest-sharing in 10, and with these relationships in all cases following intense agonism (section 5.3.2.1) serves to verify Davis' (1973) conclusions regarding hierarchical ranking in O. irroratus. Dominance hierarchies require that subordinates are able to appease conspecifics which threaten attack (Ewer 1968). Submission (section 4.3.3) was particularly evident in non-reproductive O. irroratus in response to aggression by reproductives, and in the final captive study analysis (section 5.3.2.2) the reproductive/non-reproductive combination proved relatively highly sociable. The relatively low reproductive/non-reproductive association in the field (section 5.3.1.2) probably relates to the ability of free-living non-reproductives to escape the attentions of reproductive animals, which was impossible in captivity. This aspect is discussed further in subsection C (below).

Submission was rarely observed in encounters in which the animals were approximately evenly matched, although signalling may have occurred which was too subtle for identification. This was possibly the case in the only scrotal/scrotal dyad to develop an amicable relationship (section 5.3.2.1), where the animals were of similar size (184g and 175g) and were at first equally aggressive, but by the fifth observation period were totally amicable and nested together.

The fact that 21 dyads did not develop amicable relationships and largely avoided contact after the first observation period (section 5.3.2.1) supports Davis' (1973) contention that O. irroratus is at least partially territorial. This probably applies in particular to reproductives of the

same sex (section 5.3.1). Davis (1973) found intrasexual territoriality (in reproductives only) to be less well defined in females than males, but although my encounter data contradict this (section 5.3.2), O. irroratus males are less likely to develop intrasexual amicable relationships while competing for breeding rights in the field than in dyadic combination in the laboratory. My data suggest selection favouring increased intrasexual territoriality in reproductive females relative to males, the pressures involved stemming from direct impingement on behaviour of the female reproductive strategy (see subsection B, below).

Non-aggressors of all four castes typically defended their nest-boxes against aggressors, which were rarely able to enter (section 4.3.3). This behaviour may correspond to territorial defence of small areas around the nest in free-living O. irroratus, referred to above.

Davis (1973) produced no direct evidence for temporal territoriality in O. irroratus. However, in the present field study no two animals of the same sex were captured at a particular station at the same time, although intrasexual captures were on occasion made at adjoining stations at the same time, or at the same station but at different times within the 48h period stipulated as indicating association (section 5.2.1). This at least implies a temporal restriction on the presence of one animal by that of another of the same sex, and may be sufficient to postulate intrasexual temporal territoriality, the pattern fitting that described in section 5.4.1. This interpretation does not affect the probability that O. irroratus defends the immediate vicinity of the nest as a territory in the sense of Burt (1943).

B. Mating strategy

The high level of intersexual association in the field (section 5.3.1.2), particularly that of scrotal males and perforate females (section 5.3.1), and high amicability in encounters, including early cessation of agonistic interaction (section 5.3.2.2), were almost certainly related to breeding or potential breeding in animals which were not sexually mature. Further, the high reproductive/reproductive association (section 5.3.2.2) and moderately high scrotal/scrotal association (section 5.3.1) imply active competition for mating opportunities between male O. irroratus.

Perforate females and non-scrotal males were moderately associated in the field (section 5.3.1) and relatively highly amicable in captivity (section 5.3.2.1), indicating precocial male interest in sexually available females. However, the relatively low association levels of imperforate females with scrotal and non-scrotal males (section 5.3.1) suggests general male attraction to sexually mature rather than immature females.

The zero association between scrotal males and juveniles (section 5.3.1) and the fact that eight of the 12 juvenile associations were with perforate females, presumably their mothers, suggest that lactating females do not associate with reproductive males except for mating, hence only during oestrus. This situation may derive from a male threat to neonates, as in captivity (section 5.3.2.1). These factors, together with multiple home-range overlap (Davis 1973), suggest a promiscuous breeding system in O. irroratus, although dominant males would presumably have higher reproductive success than subordinates. A male threat to neonates further implies that mating occure at some distance from the maternal nest, in which the young are left during the mother's solicitation of a mate.

Alternatively, since in the laboratory the female was unable to prevent the male from entering her nest-box or attacking her young (section 5.3.2.1), it is possible that mating occurs in the vicinity of the maternal nest, from which the young flee during the male's presence. However, this interpretation may be invalidated by the necessity of assuming the post-partum oestrus to occur later in this species than is normal in rodents, since the motor capabilities of young O. irroratus are relatively poorly developed until about five days of age (Davis 1972). Regardless of where copulation takes place, mating is probably unaffected by the occurrence of nipple-clinging in O. irroratus (FitzSimons 1920; Meester & Hallett 1970; Davis 1972), as the young do not remain permanently attached even in the first days after birth (Davis 1972).

It was postulated (subsection A, above) that breeding females are intrasexually more highly territorial than males. Apart from the immediate necessity of defending the young, increased intracaste aggression in reproductive females (section 5.3.1) may be seen as discouraging their breeding in close proximity to one another. This would ultimately provide the young with adequate food supplies and space for establishment, and may be an important factor relating to their dispersal over an average distance of only 18.3m (Davis 1973).

C. Dispersal

The low level of reproductive/non-reproductive association (section 5.3.1.2) appears to reflect the ability of free-living non-reproductives to avoid contact with reproductives (subsection A, above). Hence, while the captive study showed the existence of mechanisms (e.g. well developed appeasement behaviour) whereby some young animals would be able to establish

themselves in the vicinity of the breeding stock, others may respond to reproductive aggression by emigrating. There is obvious value in some non-reproductives being assimilated into the resident population, in that a pool of potential mates would exist to replace animals disappearing from the breeding population. Further, in terms of the theory of kin selection (Hamilton 1964; Maynard Smith 1964) the animals least likely to emigrate would be those attempting to establish home ranges overlapping those of the mother and other close relatives, full siblings in particular. The mechanism permitting such establishment would be the lower level of agonism which would be expected in an assemblage of this nature relative to that which would be experienced elsewhere in the community. This does not imply that the species characteristic of high potential aggression would be entirely lacking in such a group.

In addition to the inducement to emigrate referred to above, the non-reproductive/non-reproductive assemblage largely avoided contact in captivity (section 5.3.2.2) and was poorly associated in the field (section 5.3.1). This apparent lack of attraction between non-reproductives suggests them to be internally dispersed according to strong mutual repulsion. While reproductive/non-reproductive socialization may actively precipitate emigration (above), passive mutual avoidance by non-reproductives may be more important in this respect, generating sufficient social pressure within the group to necessitate a high rate of emigration of "recently matured animals" (Davis 1973, p. 52). It is significant that within seven days of birth some important patterns of agonistic behaviour typical of the species have emerged in O. irroratus, and are used to repel siblings (Davis 1972).

The moderate association between sub-adults and reproductive females (section 5.3.1) apparently reflects the short distance of dispersal from

the birth-site of those young able to establish themselves (subsection B, above). However, the lack of association between sub-adults and juveniles (section 5.3.1) implies that breeding females are intolerant of an earlier litter in the presence of a later one in the immediate vicinity of the maternal nest, so that dispersal may occur in response to female aggression during advanced pregnancy. (This reasoning is expanded upon in relation to dispersal in R. pumilio; section 5.4.2.2C.)

Optimum O. irroratus habitat, at least in the Natal midlands, is often restricted to narrow belts of isolated riverine vegetation (section 3.4.4.2) and high mortality of emigrants would be expected, as may be the general case for the species (Davis 1973). However, in order to explain species integrity between relatively isolated societies it is necessary to assume gene flow via the survival of some emigrants, and their reproductive success in other societies. Considering the relative dependence of O. irroratus on mesic habitats and the concomitant difficulty of crossing drier areas (section 3.4.4.2), coupled with the low probability of gaining social acceptance in a new society, the rate of genetic exchange in this species is likely to be low.

5.4.2.2. R. pumilio

A. Dispersion

The social organization in an artificial enclosure of R. pumilio from the Transvaal highveld was described by Marais (1974) as a complex of female intrasexual territoriality and male hierarchical ranking. Brooks (1974) largely supported these findings for a free-living population on the Transvaal highveld, but added that there is a slight tendency for males

to use exclusive areas at the height of the breeding season, and that both males and females tend to aggregate when not breeding (section 5.4.1). In a study on a confined colony of R. pusilio from the Cape Flats, it was found that the social system of this species is based on a male dominance hierarchy, with territoriality in alpha males and pregnant females; social organization in a free-living population was similarly structured (Johnson 1980). In view of the above, Choate's (1972) suggestion that male R. pumilio are highly territorial is open to question. However, Choate's report dealt with R. pumilio in Zimbabwe, raising the possibility of extreme regional variation in modes of dispersion in this species. This is supported by Nel's (1975) report that R. pumilio tends to form aggregated social groups in the Kalahari.

R. pumilio tends towards direct, unritualized aggression (section 4.4.2), and although appeasement behaviour appears relatively poorly developed (section 4.3.3), at least partially amicable relationships developed in all but two dyads in captivity, and nest-sharing was observed in 17 (section 5.3.2.1). The probable reasons for the discrepancy between the finding that this species was relatively highly amicable in captivity (section 5.3.2) but relatively poorly associated in the field (section 5.3.1) are set out in section 5.4.1.

The most feasible explanation for the moderate male/male association at Dargle (section 5.3.1.2) is that hierarchical ranking operates in males (Brooks 1974; Marais 1974). This system may be seen as reducing levels of direct conflict (once relative dominance has been established) in males which probably meet frequently as a result of reproductive competition between them (subsection B, below). However, in the absence of well developed appeasement behaviour, as occurs in O. irroratus (section 5.4.2.1), it is

Table 3. Continued.

DARGLE GRASSLAND	DARGLE PLANTATION	DARVILL
Setaria sphacelata		
Themeda triandra		
Trachypogon spicatus		
CYPERACEAE		
Carex zuluensis	Carex zuluensis	Cyperus immensus
Fuirena pubescens	Cyperus albo-striatus	
Kyllinga odorata		
Mariscus sieberanus		
Scirpus costatus		
JUNCACEAE		
Juncus effusus		
TYPHACEAE		
		Typha latifolia
IRIDACEAE		
Crocosmia pottsii		
Watsonia densiflora		
AMARANTHACEAE		
	Achyranthes sicula	
ASCLEPIADACEAE		
Schizoglossum hamatum		
BORAGINACEAE		
Cynoglossum lanceolatum		

Continued overleaf

likely that, if attacked, subordinates would flee rather than submit (section 4.4.2). The type of relationship observed in the captive study, in which 10 male/male dyads engaged in amicable interaction, and four nested together (section 5.3.2.2), seems unlikely to develop between free-living males in the breeding season. Excluding the combinations apparently engaged in reproductive activity (subsection B, below) most were poorly associated in the field (section 5.3.1), so it is improbable that the relatively high scrotal/scrotal index reflects affinity. Rather, it appears that more than one reproductive male was attracted to each of a limited number of potential mates (subsection B, below).

Females were totally unassociated in the field (section 5.3.1.2), and are clearly intrasexually territorial when breeding (Brooks 1974; Marais 1974; Johnson 1980). This would apply to reproductives rather than non-reproductives, but imperforate females were similarly unassociated with one another (section 5.3.1). Avoidance of contact in this caste may possibly be explained in terms of precocial intrasexual territoriality related to rising oestrogen levels prior to puberty (subsection B, below).

The high number of juvenile captures (49) occurred mainly during a capture-mark-recapture procedure adopted in January 1977 (section 3.2.1.2), and appeared to be the result of trap-proneness of that caste. Since O. irroratus was being simultaneously monitored it was not feasible to remove traps in which particular animals were repeatedly captured (Brant 1962). Baited traps are generally attractive to rodents (Fitch 1954; Patric 1969; Delany 1971; Flowerdew 1976), and juvenile R. pumilio possibly revisited trap-stations simply to obtain food. However, it seems as likely that juveniles were attracted to particular stations by conspecific odour (section 3.2.1.2) as by availability of food. As a result of this

uncertainty the high juvenile/juvenile association index (section 5.3.1) may be regarded as suspect, but for the present will be taken to infer strong intracaste juvenile affinity. This is reasonable since judging by the masses of associating juveniles, most were probably littermates.

Both encounter (section 5.3.2) and field data (section 5.3.1) suggest that non-reproductives would be largely incapable of entering a cohesive overwintering complex (Brooks 1974). However, some intrasexual dyads involving non-reproductives achieved partial amicability, and although interaction frequencies were generally low (section 5.3.2.2), the implication is that a small proportion of young animals would be able to overwinter in close proximity to other R. pumilio. Appropriately, those young born toward the end of the breeding season (immediately prior to winter) would be expected to have increased opportunities for entry into a refuge complex. This would result from rising adult agonistic thresholds (i.e. a declining propensity for agonistic behaviour) associated with post-reproductive recession of the gonads.

B. Mating strategy

High overall male/female amicability in the laboratory (section 5.3.2.2), with courtship in all intersexual encounters but one (section 5.3.2.1), permits the conclusion that high association of free-living males and females (section 5.3.1) related directly to breeding. As in O. irroratus (section 5.4.2.1), high male/male and reproductive/reproductive association in R. pumilio (section 5.3.1.2) strongly suggests that males of this species compete for mating opportunities.

The relatively low association of scrotal males with perforate females, and negligible association with juveniles (section 5.3.1), make it likely

that male/female relationships are only for the purpose of mating, and that pair-bonding does not normally occur. Marais (1974) noted that young R. pumilio are never killed by males. This suggests that absence of pair-bonding is related to promiscuous maximization of reproductive success, and not to female defence of her young, as postulated for O. irroratus (section 5.4.2.1). By virtue of multiple intersexual home range overlap (Brooks 1974) female R. pumilio are also likely to mate promiscuously, but locally dominant males (subsection A, above) probably have higher fertilization rates than submissives. Relative immobility of females during the breeding season (Brooks 1974) suggests that mating occurs in the vicinity of the maternal nest. Lack of male aggression toward young may have evolved to facilitate mating while the mother remains close enough to protect her young against other females. However, prolonged male presence may have the effect of the young being abandoned or killed by the mother, as in captivity (section 5.3.2.1).

The dispersed social system of breeding R. pumilio females (subsection A, above) implies a reproductive advantage to animals of both sexes which are capable of precipitate mating during chance meetings. The phenomenon whereby energy expenditure in courtship declined with time (sections 4.4.3, 5.3.2.1) is likely to be more defined in free-living than in captive animals. Minimizing time investment in courtship would provide a selective advantage to females by increasing the number of litters produced per unit time, and to males which curtail attention to females in sustained anoestrus and seek mating opportunities elsewhere, by increasing their fertilization rates relative to those of competitors (Parker 1974). This would explain why female R. pumilio may be induced to enter oestrus soon after meeting a suitable mate (section 4.4.3), as well as explaining the apparent reproductive strategy of the male. The mechanism described above

may be reinforced by the fact that females become aggressive toward conspecifics soon after mating (Marais 1974), which would presumably deter males from courtship of pregnant females, as in captivity (section 5.3.2.1). In Marais' (1974) study over 80% of adult females were normally pregnant at a given time, and this may provide a further reason for relatively low scrotal male/perforate female association in the field (section 5.3.1).

Reflex ovulation is known in a number of mammals (Ewer 1968), including some rodents (Foster 1934; Greenwald 1956), and appears to occur in R. pumilio, the appropriate neural stimuli being provided by the courtship "display" of the male (section 4.3.5). In addition to evidence given above for reflex ovulation (relating to reduced time investment in courtship), its existence is further implied by the fact that mating may occur at any time of the day. In contrast, spontaneous ovulators are usually more specific in the timing of oestrus, as in Rattus norvegicus (Everett 1956) and possibly P. natalensis (section 5.4.2.3). Reflex ovulation in Rhabdomys pumilio would presumably have evolved together with the reduced time investment strategy of the male as a mechanism ensuring that chance meetings between reproductive males and females would be more likely to result in pregnancy than if timing of oestrus imposed limits on the chances that mating would occur.

Free-living imperforate females appear sexually acceptable to both scrotal and non-scrotal males (section 5.3.1), as in captivity (section 5.3.2.1). Involvement in sexual activity of prepubertal R. pumilio appears to have evolved to accelerate onset of reproductive maturity in both males and females (section 5.3.2.1), as evidenced by the higher time investment in courtship observed in dyads in which one partner was in reproductive condition while the other was not (section 5.3.2.2). High time investment

in courtship of imperforate females by scrotal males may relate to female odour. Sex pheromones are well known in rodents (Carr et al 1965; Johnston 1972, 1974; Hayashi & Kimura 1974), and are controlled by oestrogen levels (Hayashi & Kimura 1974). Since oestrogen secretion commences before puberty (Everett 1961), it is reasonable to assume the appearance of specific pheromones which act as indicators of approaching reproductive capability, and which stimulate increased male time investment in courtship.

The high level of sexual interest of captive non-scrotal males in perforate females (section 5.3.2.2) contrasted with their zero association in the field (section 5.3.1). The mechanism by which non-scrotal males may be prevented from courtship of perforate females probably involves direct agonism by scrotal males, as in encounters, and would explain the negligible scrotal/non-scrotal association index.

Higher time investment in courtship by captive non-scrotal males of perforate compared to imperforate females (section 5.3.2.2) suggests that male R. pumilio are discriminating even when sexually inexperienced. In contrast, lack of discrimination by sexually naive males is known in Rattus norvegicus (Carr et al 1970) and Mus musculus (Hayashi & Kimura 1974), and may relate to androgen differentials which are governed by differences in sexual experience (Taleisnik et al 1966). The golden hamster Mesocricetus auratus is discriminating even when sexually inexperienced (Johnston 1974). While the social systems of R. norvegicus and Mus musculus are highly cohesive (Barnett 1963), that of Mesocricetus auratus appears to involve territoriality and strong mutual repulsion (Eisenberg 1966), as in Rhabdomys pumilio (subsection A, above). Since R. pumilio, Rattus norvegicus and Mus musculus are murids, and Mesocricetus auratus cricetid,

the above facts suggest the possibility of a correlation between social organization (rather than taxonomic affinity) and the ability of naive males to discriminate between reproductive state in females. In Rhabdomys pumilio, and possibly M. auratus and other rodents with similar social organizations, the adaptive function of such discrimination probably relates to maximizing male reproductive efficiency by increasing time investment in courtship of females which are likely to rapidly become receptive, relative to those which are not.

C. Dispersal

The tendency for mutual avoidance (section 4.3.3) in non-reproductive/non-reproductive encounters (section 5.3.2.2), and the low overall affinity of this complex at Dargle (section 5.3.1.2), suggests that high densities of sexually immature R. pumilio in free-living societies would cause emigration of some. However, reproductives and non-reproductives were generally poorly associated as well (section 5.3.2.2), and in addition, attempts by non-aggressors to escape from captivity (section 4.3.3) were far fewer in non-reproductive than in reproductive/non-reproductive encounters. Marais (1974) also observed attempts by non-aggressors to escape from his enclosure in response to adult aggression, and Brooks (1974), summarizing Marais' (1974) data, suggested that in free-living populations non-aggressors would emigrate. This view is almost certainly correct.

Brooks (1974) did not specify the age/mass at which emigration most commonly occurs. Although mechanisms apparently exist whereby emigration of non-scrotal males and imperforate females may be precipitated (section 4.3.3), the bulk of large-scale movements probably involve younger animals, according to the reasoning set out below.

The high juvenile/juvenile association index (section 5.3.1) apparently reflects high sibling affinity which may parallel that of Mus minutoides, for which Willan & Meester (1978) postulated group dispersal, with a litter leaving the maternal nest at about the time the next is born. However, juvenile R. pumilio were, in addition, moderately associated with perforate females (section 5.3.1), presumably their mothers. In Marais' (1974) enclosure experiment territorial females frequently killed the young of other females, and in the field an adult R. pumilio (presumably a female) was observed to attack an unguarded nest and kill and partially consume the young occupants (Flockemann 1976). In the present study mothers tolerated an earlier litter in the presence of a later one, although a third did not survive (section 5.3.2.1). These facts suggest female tolerance of her own weaned young in her territory, but they would be unlikely to nest with the mother and new litter. The upper juvenile mass recognized in this study (24.9g; section 2.2) is reached at about 40 days (Brooks 1974), which would coincide with late pregnancy, and probably increased aggression in multiparous females. It also coincides almost exactly with weaning of the second litter (mean interval between litters of 25.4 days, plus 16 days to weaning; Brooks 1974). Judging by the laboratory pattern, the mother is likely to expel the original litter from her territory at about this time, allowing the second to replace it.

If the above assessment is correct it would explain why all subadult (25-34.9g) indices were low (section 5.3.1), since leaving the mother's territory would necessitate entering the contiguous ones of other, hostile females, in which the subadults might be attacked. This mechanism would probably be reinforced by aggression by scrotal males, or at least by approaches to which the young might overreact, as in some intrasexual reproductive/non-reproductive encounters (section 5.3.1), and may be seen

as resulting in large-scale subadult movements away from centres of reproductive activity.

R. pumilio weigh only about 10g at weaning (Brooks 1974), and are certainly less fit than at the suggested second-phase dispersal mass of 25g. Evolution of a two-phase system would be expected to have been selected for by higher survival of those young which remained in the mother's territory for an additional period after weaning, compared to those which did not.

Both Brooks (1974) and David (1980) recorded high rates of disappearance of R. pumilio from their study areas, citing predation and emigration as the major contributing factors. Brooks did not give values for emigration, but estimated immigration at 12-31%/month; David estimated immigration at 25%/month. These values may approximate emigration as well, since a particular area in reasonably homogeneous habitat is likely to experience similar rates of movement in all directions. Brooks showed that all large-scale movements away from his grid were undertaken by males, and David that twice as many males as females undertook such movements. It seems likely, therefore, that gene flow in R. pumilio results largely from male rather than female dispersal. Evolution of this system may be explained in terms of the different modes of dispersion of males and females. Intrasexual territoriality in females (subsection A, above) would largely preclude immigrants of the same sex from becoming established in optimal breeding areas. In contrast, since intrasexual male socialization involves hierarchical ranking, immigrant males might be expected to survive and compete for mating opportunities in any area once they were fully mature.

5.4.2.3. P. natalensis

A. Dispersion

P. natalensis is regarded as highly sociable (Coetzee 1975, citing various authors). The present study substantiates this, with nest-sharing in 35 of the 39 dyads in which amicable interaction was observed (section 5.3.2.1), and high overall association in the field (section 5.3.1.1). De Wit (1972) found no evidence for territoriality in a free-living population, except that female home-ranges did not overlap for a three-month period during the breeding season. The social organization of P. natalensis in an artificial enclosure which was too small (6.7m^2) to permit the study of territoriality was found to be based on hierarchical ranking (Cilliers 1972), with the structure of the hierarchy dependent on demographic factors (below). The mechanisms facilitating social cohesion in this species appear to be determined by its high agonistic threshold (section 4.3.3) and partial ritualization of aggression (section 4.4.2). However, within the framework of generally high sociability, considerable variation exists which has not been adequately explained in earlier reports.

Before discussing the results of the present study, it is necessary to outline those of Cilliers (1972) who demonstrated extreme lability in P. natalensis social organization in response to population density and age structure. Such lability would be expected of a species which is subject to periodic irruptions, as is P. natalensis (section 1.2.7). A similar phenomenon has been observed in enclosed colonies of Mus musculus (Crowcroft & Rowe 1957) and Rattus norvegicus (Barnett 1963). In contrast, while social organization in a confined Rhabdomys pumilio colony varied to some extent with population demography, basic spacing mechanisms remained

relatively unaltered (Marais 1974). By approximately matching age structure in the Darvill sample against the appropriate age structure and social phase in Cilliers (1972) study, it is possible to establish the probable social mechanisms which would have underlain the indices of association reported in this study (section 5.3.1).

Cilliers' (1972) study commenced with the introduction of five male and five female P. natalensis, all adults or subadults of unknown relatedness, into an enclosure equipped with adequate shelter, food and water. During the first (three-month) phase of the experiment a single male weighing over 40% more than any other animal killed the remaining males as well as three females, was totally dominant, and was the only male to achieve copulation, although only one litter survived. Females probably killed their own young (Cilliers 1972), which they are known to do under conditions of social stress (Choate 1972). Attempting to establish a Rattus norvegicus colony using adult stock may also result in uncharacteristic conflict, resulting in elimination rather than subordination of other animals (Barnett 1963). In P. natalensis the second (five-month) phase was characterized by rapid population growth, the result of all litters surviving. By the end of the period 148 animals were present, 12.8% of them adult, and all were descendants of the original dominant male and two females. As the young matured, conflict ensued which was of lower intensity than during the first phase, and the original alpha male was gradually supplanted from his dominant position by a group of four or five large males which did not fight among themselves. The third phase lasted three months, after which half of the population was sacrificed. During this period there were no surviving litters, the population declined to 116 animals (97.4% adults), and a group comprising six males and six females dominated the colony, did not fight among

themselves, and were responsible for most reproductive effort. As in the first phase, damaging fights took place, and over 20% of the population was eliminated by the alpha group. Removal of half of the population (above) one month before terminating the experiment resulted in a reduced number of attacks by the remaining dominants on subordinates, and renewed survival of young. Choate (1972) also recorded group formation in a captive P. natalensis colony, but did not elaborate on dominance or group composition.

No attempt was made by Cilliers (1972) to explain his findings in terms of natural P. natalensis societies. However, it is clear that the first phase outlined above would be unlikely to occur in nature, except possibly following a catastrophy (e.g. flood) in which a few unrelated animals were obliged to occupy a small refuge habitat. Even then it is likely that subordinates which were frequently attacked would emigrate despite the risks involved in entering unsuitable habitat (Krebs 1978). Similarly, dispersal of subordinates would be expected to prevent the third phase being reached except during an irruption (section 1.2.7) or other exceptional circumstances (below), when emigration might be impossible due to all surrounding habitat being occupied (Kingdon 1974). In such a case the third phase density regulation mechanisms described by Cilliers (1972) would be expected to contribute to eventual population decline.

The Darvill population was relatively highly mature (i.e. with a large proportion of adults: 64.7% of captures used to calculate indices of association were of animals weighing 35g or over, and hence were regarded as adult; section 2.2). At least three of the 13 perforate females captured were pregnant, and 11 scrotal males were present, showing the population to have been reproductively active. This was in keeping with the fact that trapping at Darvill was undertaken during April and May, during the period

of maximum reproductive activity and recruitment of young (Coetzee 1967; De Wit 1972). Although it was impossible to estimate numbers of unweaned young, the proportion of weaned juveniles (14.7%) was surprisingly low, and implies low nestling survival. There was no evidence for high predation rates, but the study area was situated in more or less homogeneous habitat throughout which pilot trapping (section 3.2.1.1) had shown the presence of high numbers of P. natalensis. It is possible, therefore, that migration was restricted by population pressure in areas surrounding initial home ranges, or that emigration was neutralized by immigration. In either event, high juvenile mortality (above) may have been the result of social instability, as in phase three of Cilliers' (1972) study. If this was so then the P. natalensis dominance hierarchy would be expected to have been maintained by alpha animals of both sexes. These would have been the largest animals (Cilliers 1972), namely scrotal males and perforate females, which, judging by the appropriate indices of association (sections 5.3.1, 5.3.1.2), would have had relatively little contact among themselves.

Indices of association for caste combinations which included reproductives were generally far lower than those in which reproductives were not included (section 5.3.1); the means for the two sets of indices were 41.6 and 158.2 respectively. In addition, all indices for combinations which included reproductives were lower than those for combinations which did not (section 5.3.1). These data strongly imply that these two classes (i.e. combinations respectively including and excluding reproductives) represented discrete social groups, with relative isolation and association (section 5.2.2) respectively characteristic of reproductives and the other four castes. The mechanism by means of which such a system would be expected to operate would involve high aggression (within the constraints of a generally high agonistic threshold) in reproductives relative to the remaining castes.

The laboratory findings (section 4.3, 5.3.2) were in some respects inconsistent with the above explanation of social organization in free-living P. natalensis. However, conflict appears to relate mainly to competition for mating opportunities (Cilliers 1972), which was impossible in the present dyadic captive studies. Hence, while such competition may be indirect (subsection B, below), free-living reproductives are probably less intrasexually compatible than was the case in captive dyads.

Veenstra (1958) notes that in no circumstances does P. natalensis engage in damaging fights, but his trials were apparently conducted in similar fashion to my own. In addition, his observations involved animals from a long-established captive colony, and the possibility exists that they had prior familiarity with one another. Neighbour recognition is known to reduce conflict in Peromyscus leucopus, which is relatively sociable, but not in P. maniculatus, which is less sociable (Vestal & Hellack 1978). Hence, in the highly sociable Praomys natalensis animals (viz. neighbours) which recognized one another might be expected to engage in lower frequencies of less intense agonism than ones which had not previously met. The high agonistic threshold in P. natalensis appears not to be restricted to captive animals, since Choate (1972) reports that while family groups normally occupy a single burrow in the field (subsection B, below), adult males may also be found nesting together.

De Wit (1972) reported that with the exception of breeding females, home range overlap in P. natalensis occurs independently of the sex and age of the animals involved. However, while my field data agree with those of De Wit in respect of sex, it appears that dispersion at Darvill was highly dependent on reproductive condition (section 5.3.1.2). ("Reproductive condition" as here understood is more or less synonymous with "age" in De Wit's work.) The reason for the disparity may lie in the

different age (i.e. reproductive condition) structures of the two populations. During the 12 months of De Wit's study an average of 7.9% of animals were of a mass (40g) regarded as indicating that they were sexually mature, while 17.3% weighed 35g or over, the mass I used to indicate reproductive maturity (section 2.2). During April and May, the months in which trapping was undertaken at Darvill, De Wit's 40g and 35g averages were 2.5% and 9.2% respectively. Hence, the population studied by De Wit appears to have remained in the second demographic and social phase (Cilliers 1972) for the whole year of the study. It follows that social pressure would have been lower than in the Darvill population, with alpha animals less highly aggressive, thus facilitating non-agonistic contact between animals of both sexes and all ages. De Wit (1972) reported that emigration from his study area was not a significant cause of loss of animals from the population. However, a number of potential predators were present in the area, and although their effect was not ascertained, it seems likely that predation was a major factor limiting individual survival to an estimated 2% over a six-month period (De Wit 1972), and hence maintaining the population in a state permanently approximating Cilliers' (1972) second phase.

P. natalensis social organization is clearly based on hierarchical ranking (above). However, lack of home range overlap in breeding females (De Wit 1972), elimination rather than subordination of competitors in some circumstances (Cilliers 1972), and evidence from the present field study (section 5.3.1) combine to suggest that this species may be partially territorial, with the territorial initiative held by reproductives of both sexes. While dominants probably avoid conflict among themselves, potential aggression toward other members of the alpha group would be expected to increase in the vicinity of the home nest. Dominants did not nest together in Cilliers' (1972) study, but rather were dispersed among nest-boxes

containing subordinates. There is at this stage no evidence for group territoriality in P. natalensis, but future research may show the existence of this phenomenon, as in Rattus norvegicus (Barnett 1963) and Mus musculus (Lidicker 1976).

B. Mating strategy

Reproductive activity in the laboratory was restricted to animals which were sexually mature (section 5.3.2.1). It seems likely that this situation is well defined in free-living P. natalensis, with large dominants making the greatest reproductive contribution, as in Cilliers' (1972) colony (subsection A, above). Moreover, both the present study and that of De Wit (1972) showed male/female affinity to have been no greater than in the male/male and female/female combinations (section 5.3.1.2), suggesting that males do not compete directly for mating opportunities, as postulated for O. irroratus (section 5.4.2.1) and Rhabdomys pumilio (section 5.4.2.2). Rather, competition may be for improved position in the dominance hierarchy which, once achieved, would facilitate increased fertilization rates (Cilliers 1972).

The low intensity but high duration courtship of P. natalensis (sections 4.3.5, 5.3.2.1), during which females were generally compliant but were not evidently induced to enter oestrus (section 4.4.3), appears to relate to the essentially cohesive social organization of this species (subsection A, above). In such a system average rates of male/female interaction are likely to be high (Parker 1974). Hence, selection pressures such as those responsible for the postulated R. pumilio mating strategy (section 5.4.2.2) would appear not to function in the case of P. natalensis, and spontaneous ovulation would have evolved, rather than time-saving courtship and associated

reflex ovulation. While mating in this species always occurs at night (Cilliers 1972), the sample size in the present study was too small to ascertain whether the timing of oestrus was as specific as in other spontaneous ovulators (e.g. Rattus norvegicus; Barnett 1963). Hence, there is no direct evidence for spontaneous ovulation in P. natalensis. However, selection appears to have favoured prolonged male sexual availability, sustained by a complex of solicitous behaviour in anoestrus females (section 4.3.5). In addition, intermittent involvement of both males and females in courtship (section 4.3.5) appears to reflect the operation of selection pressures which also led to evolution of social cohesion in this species (subsection A, above).

Rodents such as P. natalensis in which prolonged courtship occurs (sections 4.3.5; 5.3.2.1) are generally monogamous (Dewsbury 1975; 1979; section 4.4.3); D.H. Gordon (Pers. comm.) suspects that pair-bonding occurs in P. natalensis. However, this was not the case in Cilliers' (1972) study, although in the initial stage of phase two, when the breeding colony comprised one male and two females (subsection A, above), a polygynous system obtained. Thereafter, dominant males achieved the majority of matings in a promiscuous breeding system. The existence of a similar system in free-living P. natalensis is implied by the low scrotal/perforate index of association (section 5.3.1), but it is interesting to note that if the dominant male group comprised siblings (as in Cilliers' study) the system would approximate polygyny in the genetical sense. Apart from the obvious selective advantage to dominant males achieving high fertilization rates, an advantage would also accrue to females with which they mated. This would occur through the young inheriting genes favouring their own future dominance, and hence reproductive success.

In O. irroratus and Rhabdomys pumilio, juveniles were moderately associated with perforate females, from which it was concluded that systems of protracted maternal care operated in those species (respectively, sections 5.4.2.1; 5.4.2.2). However, in P. natalensis the two castes were relatively poorly associated (section 5.3.1), implying that maternal care in this species does not extend beyond weaning.

C. Dispersal

In the cases of O. irroratus (section 5.4.2.1) and R. pumilio (section 5.4.2.2) there appeared to be evidence that the bulk of large-scale movements at Dargle would have been undertaken by non-reproductives. The mechanisms obliging young animals to emigrate apparently related broadly to aggression of reproductive adults, and to non-reproductive/non-reproductive mutual avoidance.

Emigration may have been of minor importance in limiting population growth of P. natalensis both at Darvill (subsection A, above) and in De Wit's (1972) study, and it appears that mechanisms such as those referred to in the above paragraph may not operate in this species. This is suggested by high non-reproductive/non-reproductive and reproductive/non-reproductive amicability in captivity (section 5.3.2.2) and association in the field (section 5.3.1.2). Reproductive/reproductive scores were low in both cases (sections 5.3.1.2, 5.3.2.2), and mutual repulsion between reproductives, which may provide a basis for partial territoriality in this species (subsection A, above), might also give impetus to emigration of animals in reproductive condition. Judging by the relatively low scrotal/scrotal amicability in encounters (section 5.3.2.2), their negligible association in the field (section 5.3.1), and the high incidence of inter-male conflict reported by Cilliers (1972), the majority of animals

leaving the parent group would probably be scrotal males.

The hypothesized system of dispersal described above closely parallels that of Mus musculus, in which adult males were the most frequent emigrants from social groups in a large (385m²) enclosure (Lidicker 1976). Males were rarely able to enter another group, although females were marginally more successful in this respect. Weaned young seldom attempted to leave the parent group.

Lidicker (1976) did not discuss the mechanisms underlying attempted dispersal in M. musculus. However, to avoid conflict with dominants, P. natalensis reproductives which were not members of the alpha group (subsection A, above) would be expected to emigrate, although their chances of acceptance in another society would be slight. This is borne out by the fact that animals entering Cilliers' (1972) enclosure from the outside were always killed. In contrast to the pressures on subordinate (and hence non-territorial, subsection A, above) reproductives to disperse, non-reproductives would not pose an immediate challenge to dominants, and would function within the society as a pool of potential mates to replace animals disappearing from the breeding stock.

M. musculus social groups resist immigrants, and hence genetic contamination, but extensive gene flow may occur as a result of formation of new groups in empty spatial and social niches (Anderson 1970; Lidicker 1976). No information is at present available on the mechanisms involved in gene flow in P. natalensis, or its extent. However, based on other similarities in the social systems of M. musculus and P. natalensis (above), and on ecological similarities (e.g. commensalism; section 1.2.5), it is reasonable to suppose that the mechanisms and rates of gene flow in the two species may also be similar.

The fact that both juveniles and sub-adults were relatively poorly associated with perforate females in the field (section 5.3.1) suggests that young leave the vicinity of the maternal nest soon after weaning. They would then be expected to remain in the society of their birth at least until sexual maturity, and thereafter to enter the dominant breeding population, to remain in submissive non-breeding roles, or to emigrate. The last course would probably occur relatively frequently at low population densities, increasing the rate of gene flow, but at high densities a large subordinate non-reproducing population would be expected, as appeared to be the case at Darvill (subsection A, above), and the rate of gene flow would be low.

6. SOCIAL ECOLOGY

6.1. Introduction

Social ecology has been defined as the study of social structure in relation to ecology (Crook 1970) and as the study of the biological basis of social behaviour (Wilson 1975; Barash 1977). The subject is thus concerned with the adaptive significance of social phenomena.

In recent years there has been increasing emphasis on the interpretation of social structure in terms of environmental parameters, although studies have concentrated mainly on species which may be easily observed in the field, such as birds (e.g. Crook 1965), large herbivores (e.g. Geist 1971; Jarman 1974) and primates (e.g. Crook & Gartlan 1966; Clutton-Brock 1974). The study of rodent social ecology was initially also confined to easily observable species, for example tree squirrels Tamiasciurus (Smith 1968) and marmots Marmota, the latter being dealt with in series of papers by Barash (e.g. 1973, 1974) and Armitage and his co-workers (e.g. Anderson et al 1976; Armitage 1977). A watershed in the ecological interpretation of social organization of cryptic rodents was provided by Happold's (1973) study, referred to in section 3.1. There have been no studies of Southern African rodents which could be described as primarily socio-ecological.

An attempt is made in this chapter to interpret social phenomena in Otomys irroratus, Rhabdomys pumilio and Praomys natalensis (sections 4, 5) in terms of the apparent habitat preferences (section 3) and other aspects of the ecology of these species. In section 5.1 reference was made to the danger of attempting to classify social organization using too many traits (Wilson 1975). It would appear equally impractical to attempt socio-ecological

interpretation using all available information. Consequently, in the following sections (6.2, 6.3) attention is mainly given to those social attributes which, on the available information, appear most distinctly adaptive.

For convenience, the summary given in section 3.4.4.2 of the apparent habitat preferences of O. irroratus, R. pumilio and P. natalensis, at least in the Natal midlands, is repeated here, as follows:

O. irroratus. Mesic areas with good vegetative cover; resource availability is variable in space (i.e. small areas of optimum habitat), but within these areas is high and stable in time.

R. pumilio. Drier areas with less dense vegetation, and with resource availability less variable in space (i.e. large areas of optimum habitat), but less stable in time (i.e. seasonally ephemeral) than in the mesic habitats favoured by O. irroratus.

P. natalensis. Disturbed habitats; availability of such habitats, and hence of resources, is highly variable in space (i.e. resulting from possibly localized chance disturbance of the environment) and time (i.e. dependent on the rate of ecological succession).

6.2. Social behaviour and ecology

6.2.1. Communication

The communicatory repertoires of O. irroratus, R. pumilio and P. natalensis (sections 4.3.1, 4.4.1) respectively appear to be dominated

by auditory, visual and olfactory signals. (This generalization is expanded upon below.)

Systems of communication are greatly influenced by light availability. Whereas diurnal mammals have good visual acuity and emphasize visual signalling (Ashby 1972), nocturnal ones have reduced the visual role in favour of other forms of communication (Eisenberg 1967). Aspects of the communication systems of O. irroratus, R. pumilio and P. natalensis observed in this study (sections 4.3.1, 4.4.1), clearly illustrate this dichotomy.

At the two extremes, the diurnal R. pumilio and nocturnal P. natalensis respectively appear to emphasize visual and olfactory communication, while the largely crepuscular O. irroratus has well developed auditory and visual elements in its communicatory repertoire (sections 4.3.1, 4.4.1). Johnson (1980) also noted well developed visual communication in R. pumilio. Visual emphasis in O. irroratus may be explained by the fact that this species exhibits considerable daylight activity, although Davis (1973) suggested that its vision is poor. This may explain why its signals tend to involve gross postural movements rather than the more subtle changes in organ disposition which predominate in the almost totally diurnal R. pumilio (Brooks 1974; Christian 1977a). This may in part be explained by semi-crepuscularity in O. irroratus and its preference for dense cover (sections 3.3.3, 3.4.2), which allows little penetration of light to its runways compared to those of R. pumilio. In consequence, social activity in O. irroratus must normally take place in dim light, necessitating improved non-visual communication, as in Microtus townsendii (Boonstra & Krebs 1976), and resulting in reduced visual acuity (Davis 1972), from which the use of large-scale movements as visual signals would be expected to have followed. However, interpretation of the prominent upright posture and tail and fore-paw movements (section 4.3.1) as largely of visual significance may be simplistic,

since the upright position in O. irroratus frees the fore-paws for warding (section 4.3.3) which is strongly tactile, and tail-quivering may provide auditory rather than visual cues (Ewer 1968; Hickman 1979), especially in narrow runways where the tail would make audible contact with the surrounding vegetation.

Probably also in response to differences in patterns of diel activity, aggressive approach (section 4.3.3) and early amicable approach (section 4.3.4) differ markedly in R. pumilio but are almost indistinguishable in P. natalensis. Similarly, aggressive and amicable approach behaviour are almost identical in O. irroratus.

R. pumilio appears to possess morphological adaptations which would facilitate signalling with the eyes and ears while O. irroratus and P. natalensis do not. In R. pumilio the eyes appear to be emphasized by pale yellow bands approximately 2mm wide above and below, which contrast strongly with the remainder of the face (section 1.2.3). Other diurnal rodents (such as Lemniscomys griselda and Paraxerus cepapi) have similar markings defining the eyes, as do at least some of the largely diurnal Macroscelididae (Pers. obs.). Such markings do not occur in P. natalensis or in other nocturnal small mammals examined (e.g. P. verreauxi, Acomys subspinosus, Aethomys chrysophilus, A. namaquensis, Dasymys incomtus, Dendromus melanotis, D. mesomelas, Mus minutoides, Saccostomus campestris, Tatera spp. and a number of Soricidae). O. irroratus does not have the eyes defined by pale markings, and Davis (1973) used the absence of this character to distinguish it from O. angoniensis, in which rings of orange hairs surround the eyes in the otherwise dark face. While O. irroratus and O. angoniensis have similar patterns of diel activity, irroratus tends to inhabit more densely covered habitats than angoniensis (Davis 1973). This appears highly significant, and supports the argument that pale markings

around the eyes have evolved to improve visual communication in small mammals active at high light intensities. The ear pinnae in R. pumilio appear to be similarly adapted since, when viewed anteriorly, the inner yellowish area contrasts strongly with the black edge (section 1.2.3) and with the head and face. No such contrasting colouration exists in P. natalensis, while in O. irroratus the ears are particularly inconspicuous.

The prominent stripes along the dorsum in R. pumilio (section 1.2.3) do not appear to play a specific role in communication, as no postures were observed in which they were emphasized. Although the characteristic pattern may facilitate recognition by conspecifics, it is likely that the stripes relate to cryptic colouration, and that they may be regarded as an adaptation to diurnal activity in poorly vegetated habitats.

The modes of dispersion of the three species are discussed in section 6.3 but it is appropriate at this stage to deal with the effects of dispersion on communication.

Territorial exclusion (Burt 1943) implies either considerable energy expenditure in boundary defence as in some birds (e.g. Lack 1954), or use of olfactory or other delimiting signals as in many mammals (Ewer 1968). However, visual emphasis in captive R. pumilio suggests that both territorial integrity in females and hierarchical dominance in males (section 5.4.2.2) may be maintained by agonistic confrontation (section 4.3.3) involving immediate visual signals rather than remote olfactory ones.

Similarly, the available evidence, although not conclusive, suggests that communication in O. irroratus may be dominated by immediate, in this case auditory, rather than remote signalling, and although marking occurs,

it apparently fails to deter conspecifics, while conspecific urine and faeces are largely ignored (Davis 1973). The adaptive significance of non-olfactory emphasis may partly relate to the mode of dispersion of this species (section 5.4.2.1), since the existence of potentially aggressive animals such as O. irroratus (section 4.3.3) in close proximity to conspecifics would necessitate awareness of their precise location in relation to one another. Such information would be less efficiently rendered by persistent scent marks than by non-olfactory signals. Further, selection for auditory emphasis conceivably occurred in direct response to the preference of O. irroratus for densely vegetated habitats (section 6.1) in which animals might be invisible to one another even when comparatively close together.

P. natalensis possesses a relatively complex marking inventory, and probably relies largely on olfactory communication. However, it is essentially non-territorial (section 5.4.2.3) and its use of odour may relate to group cohesion, as for example in Rattus norvegicus (Barnett 1963). The fact that intruders entering Cilliers' (1972) enclosure were killed probably resulted from their odour being unfamiliar to residents.

6.2.2. Agonistic behaviour

The features most descriptive of the social behaviour of the three species relate to agonistic interaction (sections 4.3.3, 4.4.2), and are as follows:

O. irroratus. Highly aggressive, but agonism is ritualized.

R. pumilio. Less overtly aggressive than O. irroratus, but agonism tends to be direct and unritualized.

P. natalensis. Agonism is poorly developed and ritualized.

Partial ritualization of aggression in O. irroratus and P. natalensis, and retention of more direct aggression in R. pumilio (section 4.3.3) appear to be adaptations which promote dispersion to suitable species-specific density levels (section 4.4.2), which are in turn limited by environmental factors. Among the many variables which may influence population size of small rodents, such as food (e.g. Bendell 1959), water (e.g. Christian 1979a) and availability of suitable nest-sites (e.g. Seely 1976), is included local availability of suitable habitat (Krebs 1978).

In the case of R. pumilio, which is primarily a grassland species with a distinct xeric tendency (section 3.4.4.1), areas of suitable habitat are extensive in the Natal midlands (section 3.4.4.2). Hence, this species may not have been subjected to selection for ritualization of aggression imposed by the pressure of limited available space. In other words, in the evolutionary history of R. pumilio animals which were obliged to emigrate from the vicinity of the birth-site as a result of direct conspecific aggression would have found themselves in a similar environment to that of the parent population, and enforced emigration would thus not have acted as a powerful agent of selection.

The optimum (i.e. mesic) habitats of O. irroratus are often of limited size (section 3.4.4.2), and animals emigrating from such areas would be strongly selected against. Selection may therefore be seen as having favoured animals which remained within the parent population, hence also selecting for ritualization of aggression to reduce levels of damaging conflict in situations of high population density. A similar argument may apply in the case of P. natalensis, particularly since favoured (i.e. disturbed) habitats were presumably less extensive and less common historically

than at present (section 3.4.4.2).

6.3. Social organization and ecology

The social systems of the three species appear to fit the following general descriptions:

O. irroratus (section 5.4.2.1). Animals live in close spatial association (i.e. the system is cohesive in space), but the probable existence of temporal territoriality (see section 5.4.1) in this species suggests that individuals may seldom meet face to face (i.e. the system is dispersed in time). In addition, breeding females are intrasexually territorial, and hierarchical relationships exist among males.

R. pumilio (section 5.4.2.2). During the breeding season dispersion is based on female intrasexual territoriality and male hierarchical ranking. There is a tendency for aggregation in mesic refuge habitats in the winter non-breeding period.

P. natalensis (section 5.4.2.3). The colonial social organization is based on dominance hierarchies, the structure of which depend on demographic factors (see section 5.4.2.3). Alpha animals of both sexes probably maintain small territories in the vicinity of their nests.

Wilson (1975) draws attention to two important ecological determinants of modes of animal dispersion. First, the area of the home range must be large enough to ensure sufficient energy for survival and reproduction,

and ideally it should not be much greater than this optimum size. Although Wilson refers specifically to energy, the area must of necessity also provide other resources such as water, nest-sites and mating opportunities. Second, modes of dispersion are dependent upon the distribution of resources in space and time, with uniform distribution favouring evolution of territoriality and patchy distribution selecting for coloniality and group exploitation of the habitat. In this respect, gradients of environmental stability were used by Barash (1974) to explain the gross differences in the social systems of three species of marmot Marmota, referred to in section 3.1. Brown (1974) lists the following three factors in addition to those above, as selecting for species-specific modes of dispersion in New World jays: intraspecific competition, susceptibility to predation, and the energy cost and effectiveness of territorial defence and foraging. Consideration of the last three factors would require detailed information which is not at present available for the species being considered here, and the following discussion is thus confined mainly to the relationship between modes of dispersion and availability and distribution of resources in their preferred habitats (sections 3.4.4.2, 5.1).

Before going on to deal with characteristic attributes of the modes of dispersion of each species, features developed to a greater or lesser extent in all three (above) are briefly discussed, namely hierarchical ranking and maintenance of territories.

Intrasexual hierarchical ranking is apparently prominent in male O. irroratus and R. pumilio, and in both P. natalensis sexes (above). Dominant animals of any species have greater access to limiting resources, and hence greater individual fitness than subordinates (Wilson 1975; Dawkins 1976; Barash 1977); reproduction is a vital component of fitness

(Stearns 1976). The fact that it is only male O. irroratus and R. pumilio, and not females, which form dominance hierarchies suggests that availability of mating opportunities is the critical resource for which competition occurs. Similarly, while both P. natalensis sexes compete to join a dominant group, reproductive success may be largely confined to this group (section 5.4.2.3).

An interesting aspect of hierarchical relationships in the three species is that they appear to represent better ordered contests in O. irroratus and P. natalensis than in R. pumilio, where flight by a non-aggressor from an aggressor is characteristic (section 5.4.2.2). This disparity apparently reflects selection in response to differences in the areas of suitable habitat available to these species (section 3.4.4.2), for the same reasons as those given in section 6.2.2, relating ritualization of aggression to habitat size.

Intrasexual territoriality appears better developed in breeding female than in male O. irroratus (section 5.4.2.1) and R. pumilio (section 5.4.2.2), while in P. natalensis this phenomenon is probably poorly represented (section 5.4.2.3). Territorial defence in female O. irroratus probably relates mainly to providing dispersing young with adequate space, and hence resources for establishment in the limited area of prime habitat available to this species (section 6.1). Such a strategy would provide a powerful selective advantage to females able to maximize their reproductive success in this way, and may be regarded as an extension of the highly efficient maternal care (e.g. nipple-dragging) described for this species by Meester & Hallett (1970). The territory of female R. pumilio is probably held to ensure the safety of the young until dispersal, probably to a relatively distant area of suitable habitat, and therefore would also reflect the inclusive fitness of the mother. Lack of well developed

territoriality in female P. natalensis apparently indicates a low level of conspecific threat to the young, at least during periods of rapid population growth (below), but also shows that parental care is poorly developed in this species.

The apparent occurrence of temporal territoriality in O. irroratus is clearly an adaptation permitting high population densities of intraspecifically aggressive animals to occupy limited areas of prime habitat (section 3.4.4.2). Similar reasoning was invoked to explain ritualization of aggression in this species (section 6.2.2). An appealing explanation for the evolution of temporal territoriality in this species stems from kin selection theory (Hamilton 1964; Maynard Smith 1964), and is based on the probability that within any small area of habitat many or most of the O. irroratus present may be closely related. Thus, temporal territoriality may represent a form of altruistic behaviour which serves to reduce the probability that close kin will emigrate into marginal environments, thereby reducing their chances of survival and reproduction, and reducing the inclusive fitness of the population. This reasoning is supported by the short distance of movement from the maternal territory of dispersing young (section 5.4.2.1).

It is interesting briefly to speculate further on the evolution of temporal territoriality in O. irroratus. During the Pleistocene, the vegetation of Southern Africa was greatly influenced by variation in rainfall associated with alternating pluvial and interpluvial periods, and mesic habitats were periodically far more extensive than at present (Cooke 1962). Evidence that the area of habitat suitable for occupation by O. irroratus has become reduced is provided by the occurrence of isolated populations of this species in the S.W. Arid and in eastern Zimbabwe (section 1.2.4). It would be expected, therefore, that the

social organization of this species, under conditions where extensive areas of suitable habitat were available, would have been based on territorial exclusion of conspecifics, as is the case in Marmota monax (section 3.1). With the gradual reduction in size of areas of available habitat, selection for reduced dispersal distance may be envisaged as having occurred, accompanied by compression of territories, leading to territorial overlap and ultimately to temporal territoriality.

O. irroratus has always been thought of as asocial (section 1.2.7), but it has recently been referred to as colonial (Perrin 1980b,c). This conclusion was at least partially based on evidence that some kin-selected, colonial New World jays are K-selected (Brown 1974), with it following that since O. irroratus is clearly K-selected (section 7.3), and probably kin-selected (above), it should also be colonial (Perrin In litt.). However Perrin (In litt.) agrees that there may be exceptions to what he regards as the general correlation between coloniality and K-selection. There is to my knowledge no evidence that O. irroratus is colonial, and on the basis of the information presented in sections 4 and 5, and by Davis 1973, the social system of this species must be regarded as dispersed rather than cohesive (section 5.1).

An important aspect of the mode of dispersion of R. pumilio (above) as it relates to habitat preferences is the tendency of this species to aggregate in the winter, non-breeding season (Brooks 1974). The whole of Brooks' study area was essentially mesic, comprising a marshy habitat in which sedges were dominant and cover averaged 83%, and a less wet area where hydrophilous grassland species predominated and cover averaged 73%. R. pumilio displayed seasonal changes in utilization of the two habitat types, and in the winter aggregation of 1970 the marshy habitat, which represented a refuge area (Brooks 1974), was preferred. In winter 1971

aggregation occurred in the grassland and not the marshy habitat which was apparently preferred for over-wintering. This was probably as a result of competitive exclusion by O. irroratus which was largely restricted to the marshy area, and was more than twice as common in 1971 than it had been in 1970 (Brooks 1974). Aggregation in winter of R. pumilio in mesic refuge habitats probably improves over-wintering success as a result of greater availability of staple resources such as food and water in mesic than in drier habitats, particularly in winter (section 3.4.4.2). It would be expected that over-wintering aggregations of R. pumilio in mesic refuge habitats would be more characteristic of this species in drier areas, or in ones where gradients of water availability were well defined, than in more generally wet areas such as Brooks' study area.

From the apparent winter preference of R. pumilio for mesic habitats arises the question of why this species does not permanently occupy wetter areas with high resource availability. Competitive exclusion of R. pumilio by O. irroratus (Brooks 1974) is probably an important factor in this connection, for while competition for food may be slight (Brooks 1974; Perrin 1980a), such resources as nest-sites (section 3.4.2) and living-space in general (Brooks 1974) may be in short supply. Another factor which possibly influences seasonality of habitat utilization in R. pumilio is that of its poor swimming ability, and the risk of occupying flood-accessible areas during the breeding season, which coincides with the period of maximum danger of flooding in the summer rainfall region (section 3.4.1). Poor swimming ability is doubtless an effect rather than a cause of habitat selection, but the short hair and lack of a buoyant "ruff" in this species (section 3.4.1) would have made the evolution of efficient swimming less likely than in O. irroratus and P. natalensis.

Abundant resources appear to be available to P. natalensis in disturbed habitats, but under natural conditions (i.e. excluding human interference) optimum areas may be localized, and their carrying capacity for this species may decline rapidly as succession proceeds (section 3.4.4.2). Hence, an area conducive to rapid P. natalensis population growth might, as succession proceeded, rapidly become so unfavourable as to either eliminate this species or reduce it to only a few survivors.

Coloniality and hierarchical ranking in P. natalensis (above), together with its high reproductive potential (section 7.2.3), are adaptations which favour maximum exploitation of available areas of disturbed habitat. Cilliers' (1972) findings in respect of a confined P. natalensis population (section 5.4.2.3) are instructive in this regard. In recently disturbed habitats where small numbers of P. natalensis were present, whether as residents in the area prior to disruption or by immigration, exponential population growth would probably occur. Rapid growth would be facilitated not only by the high fecundity of the species, but also by its colonial habit, in that oestrus females would almost certainly be mated as a result of regular social contact with the dominant male. When saturation density was reached and social conflict commenced (phase three; Cilliers 1972) emigration of subordinate animals into marginal (undisturbed) habitat would be expected, with the possibility of some emigrants surviving and reproducing in such habitats, and some possibly colonizing other disturbed areas. The course of events would be similar if, as a result of rapid plant succession and colonization by specialist competitors (Meester et al 1979), the area became unsuitable for P. natalensis.

7. LIFE-HISTORY TACTICS

7.1. Introduction

In his review of theories pertaining to life-history tactics, Stearns (1976) points out that a life-history trait or combination of co-evolved traits may be explained in terms of any one of several plausible hypotheses. It is not necessary here to undertake an exhaustive discussion of these hypotheses since Stearns (1976) has done so, while Perrin (1980b) has reviewed the major areas of life-history theory, emphasizing ideas pertinent to the breeding strategies of O. irroratus and R. pumilio.

The concept of r- and K-selection (MacArthur & Wilson 1967), as developed by Pianka (1970), has been used to explain a wide range of life-history phenomena. Pianka's model has been employed to interpret, for example, variation in reproductive rate of terrestrial Protozoa (Bamforth 1980), population stability of hibernating small rodents (Kirkland & Kirkland 1979), reduced population fluctuation (relative to other microtine rodents) of an island population of Microtus breweri (Tamarin 1978), and differences in social organization among conilurine rodents (Happold 1973). The breeding strategies of O. irroratus and R. pumilio were discussed mainly in terms of r- and K-selection (Perrin 1980b), with this author concluding that R. pumilio is r- and O. irroratus K-selected.

The theory of r- and K-selection predicts that species occupying unstable or unpredictable habitats will be comparatively r-selected and those in stable, predictable habitats comparatively K-selected. At the r- endpoint of the r-K continuum there is a theoretical ecological vacuum in which there are no density effects or competition, while the K-endpoint

represents a situation where density effects are at a maximum and competition is keen. Thus, the optimum r-strategy involves maximization of productivity by reducing body size, longevity, age at sexual maturity, parental care, size of the young and generation time, by increasing litter size and number of offspring, and by evolution of semelparity. The optimum K-strategy maximizes efficiency of resource utilization and competitive ability by increasing body size, longevity, parental care, size of the young and generation time, by delaying reproduction, by reducing litter size, and by iteroparity. Logically, no species ever achieves either the r- or K-endpoint, but each achieves a compromise position at some point along an r-K continuum (Pianka 1970).

Interpretation of life-history tactics according to r-K theory poses certain problems. Life-histories are dynamic in time, both in a unidirectional evolutionary sense, in response to long-term environmental change (Stearns 1976), and in the sense of adaptive shifts to accommodate short-term environmental variability (Perrin 1980b). A second practical difficulty is that when the correlates of r- and K-selection are examined in terms of an alternative hypothesis, named bet-hedging by Stearns (1976), predictions are generated which differ markedly from those of Pianka (1970). In essence, the bet-hedging hypothesis distinguishes between environmental impact (in unstable environments) on juvenile and adult mortality, predicting that when juvenile mortality is high selection favours increased longevity and reduced reproductive effort, but when adult mortality is high selection occurs for reduced longevity and increased reproductive effort (Stearns 1976; Perrin 1980b). There is at present little evidence to support this hypothesis, and Perrin (1980b) only noted the importance of alternative explanations for life-history tactics, while interpreting his data mainly in terms of r- and K-theory.

I elect to follow Perrin (1980b) and numerous other authors by here interpreting life-history phenomena largely in terms of r and K. This decision rests on the generally good fit of the available information on O. irroratus, R. pumilio and P. natalensis (section 7.2) to the theoretical model (Pianka 1970).

The key life-history traits, on which discussion in section 7.2 is concentrated as far as possible, are the mean and variance in age at first reproduction, clutch (litter) size, size of young, and the interaction of reproductive effort with adult mortality (Stearns 1976).

7.2. Correlates of r- and K-selection

The correlates of r- and K-selection discussed in the following sections (7.2.1 - 7.2.6) are listed in Table 43, which is modified after Pianka (1970), Stearns (1976) and Perrin (1980b). Much of the information used in this section is from the published and unpublished work (e.g. theses) of others, since I did not set out expressly to elucidate many of the parameters listed (Table 43), and my samples were often too small to be useful. It should be noted that in some instances data have been used which are only comparable in a general sense; for example, litter sizes recorded in both field and captive studies are listed and compared.

In section 7.3 an attempt is made to describe the relative positions of the three species on an r-K continuum.

7.2.1. Habitat stability

Earlier authors (section 7.2) in the context of r- and K-selection have referred to climatic stability or predictability, but where species

Table 43. Some correlates of r- and K-selection. (Modified after Pianka 1970, Stearns 1976 and Perrin 1980b.)

CORRELATES (PARAMETERS)	r-selection	K-selection
Habitat stability (predictability)	Less stable	More stable
Body size	Smaller	Larger
Longevity	Shorter	Longer
Reproductive capacity	Higher	Lower
gestation period	Shorter	Longer
generation time	Shorter	Longer
litter size	Larger	Smaller
reproductive effort (energy)	Higher	Lower
seasonality	Semelparity	Iteroparity
fertility	Higher	Lower
parental care	Less	More
Population density	More variable	Less variable
Social organization	Cohesive	Dispersed
Interspecific competition	Poorly developed	Well developed

occupy habitats within the same climatic zone (section 1.2.5), the term habitat stability is to be preferred. As outlined in sections 3.4.4.2 and 6.1, the preferred habitats of O. irroratus are relatively stable, of R. pumilio seasonably unstable, and of P. natalensis markedly ephemeral.

7.2.2. Body size and longevity

O. irroratus is far larger than either R. pumilio or P. natalensis which are of the same order of size (section 1.2.3).

O. irroratus apparently has a greater ecological longevity than R. pumilio, which in turn appears longer lived than P. natalensis (Table 44). In the context of trapping studies, the term longevity refers only to animals which remain in the study area. The maximum life span of 19 months in R. pumilio was based on the survival of only two animals out of 2281 (David 1980). The greater recorded life-span of Cape Flats R. pumilio relative to that recorded on the Transvaal highveld is probably accounted for by the fact that David's (1980) study continued for five years, while Brooks (1974) trapped monthly for only one year, with only three trapping sessions in the following year. Davis (1973) trapped concurrently with Brooks (1974), and O. irroratus probably has a greater ecological longevity than the 22 months recorded. De Wit's (1972) study took place during a period of abnormally low rainfall and in an area of apparently less than prime P. natalensis habitat. Thus, the maximum lifespan and over-wintering success of this species may be generally greater than those recorded in Table 44.

7.2.3. Reproductive capacity

The suggested gestation period of about 40 days in O. irroratus (Davis 1973) is considerably greater than that of R. pumilio and P. natalensis

Table 44. Longevity of O. irroratus, R. pumilio and P. natalensis in the areas indicated. T = Transvaal highveld; C = Cape Flats; 1 = De Wit (1972); 2 = Davis (1973); 3 = Brooks (1974); 4 = David (1980); 5 = Davis & Meester (1981).

SPECIES	LOCALITY	MAXIMUM LONGEVITY	SURVIVAL*	SOURCE
O. irroratus	T	22 months	13% for one year	2,5
R. pumilio	T	16 months	2.3% for one year	3
R. pumilio	C	19 months	1.3% for one year	4
P. natalensis	T	339 days	2% over-wintering	1

* survived and remained in the study area

(Table 45). Similarly, generation time, the sum of gestation period and age at sexual maturity, is greater in O. irroratus than in R. pumilio and P. natalensis, for which approximately the same period has been recorded on the Transvaal highveld (Table 45). However, a single record exists of a P. natalensis female producing its first litter at 77 days old (Meester 1960). Histological evidence (Baker & Meester 1977) confirms that both males and females of this species are physically capable of reproductive activity before reaching an age of 54 days, the time when the female that gave birth at 77 days old (Meester 1960) would have been mated, assuming a 23-day gestation period (Table 45). The reduced generation time of R. pumilio on the Cape flats relative to that on the Transvaal highveld (Table 45) may simply reflect the abundant food supply (mainly the highly nutritious seeds of alien acacias) in David's (1980) study area, which could result in accelerated sexual maturation. However, it is also possible that under the rigorous conditions obtaining in the S.W. Cape (i.e. the prolonged summer drought), R. pumilio has been selected for earlier breeding and thus tends to be more nearly r-selected than in less harsh environments.

(The generation times given in Table 45 refer only to young born early enough in the breeding season to permit their own reproductive activity before the onset of winter. Reproductive seasonality in the three species is discussed below.)

Mean litter size of O. irroratus appears to be less than half that of R. pumilio, which in turn is about half that of P. natalensis (Table 46). The suggested mean litter size of 10 in P. natalensis (Coetzee 1975) is higher than any other which has come to my attention, and in terms of this parameter (compared to other rodents) P. natalensis clearly tends toward the far r-extreme of the r-K continuum. This species is, in addition,

Table 45. Gestation period and generation time of O. irroratus, R. pumilio and P. natalensis in the areas indicated. T = Transvaal highveld; C = Cape Flats; 1 = Johnston & Oliff (1954); 2 = Coetzee (1967); 3 = Meester & Hallett (1970); 4 = De Wit (1972); 5 = Davis (1973); 6 = Brooks (1974); 7 = David (1980); 8 = Davis & Meester (1981).

SPECIES	LOCALITY	GESTATION PERIOD	GENERATION TIME	SOURCE
O. irroratus	T	± 40 days	4-5 months	5, 8
R. pumilio	T	25 days	3 months	6
R. pumilio	C	25 days	10 weeks	7
P. natalensis	T	23 days		1, 3
P. natalensis	T		3 months	2, 3, 4

Table 46. Litter size of O. irroratus, R. pumilio and P. natalensis in the areas indicated. T = Transvaal highveld; F = Fish River valley; C = Cape Flats; N = Natal midlands; 1 = Oliff (1953); 2 = Meester (1960); 3 = Davis (1963); 4 = Coetzee (1965); 5 = De Wit (1972); 6 = Davis (1973); 7 = Brooks (1974); 8 = Coetzee (1975); 9 = Baker & Meester (1977); 10 = David (1980); 11 = Perrin (1980b); 12 = Davis & Meester (1981).

SPECIES	LOCALITY	$\bar{X}$ LITTER SIZE	SOURCE
O. irroratus	T	2.33	6, 12
O. irroratus	F	1.48	11
R. pumilio	T	5.90	7
R. pumilio	F	4.90	11
R. pumilio	C	4.92	10
P. natalensis	T	7.3	1
P. natalensis	T	8.5	2
P. natalensis	T	7.0	3
P. natalensis	T	9.22	4
P. natalensis	T	8.0	5
P. natalensis	N	11.27	9
P. natalensis	*	10.0	8

* mean value given for the species

capable of producing as many as 17 (Meester 1960; Baker & Meester 1977) or even 19 (Coetzee 1965) young/litter.

Reproductive effort, the proportion of the total female energy budget invested in reproduction, may provide a measure of a species' position in relation to r- and K-selection (Millar 1977), and was used as such by Perrin (1980b). Estimates of reproductive effort per pregnancy are obtained by calculating

$$R_e = N W_w^{0.75} (m^{0.75})^{-1}$$

where R_e = reproductive effort, N = litter size, W_w = mass of individual offspring at weaning and m = adult mass (Millar 1977). Table 47 gives R_e values for O. irroratus and R. pumilio after Perrin (1980b) who made calculations from his own Fish River valley data and those available for the Transvaal highveld (Davis 1973; Brooks 1974), and for P. natalensis, calculated from data in Meester & Hallett (1970), Coetzee (1975) and Baker & Meester (1977). David's (1980) data were unsuitable for calculating reproductive effort as he did not include the overall mean mass of breeding females or mass at weaning, but judging by the mean litter size he gives (4.92) R_e on the Cape Flats is probably about the same as elsewhere (Perrin 1980b). In the case of P. natalensis (Table 47) Baker & Meester (1977) did not give the mean mass of parturient females, but since the animals they used were weighed at the time of capture (Pers. obs.), the mean mass of adult females at that time (41.8g) has been incorporated into the calculation. The resultant value, R_e = 4.48, is higher than all but one of the 100 mammalian R_e's given by Millar (1977), and a source of potential error in the calculation was thus sought. The mean mass of parturient females was probably higher than 41.8g, but even using a value of 50.0g (probably an

Table 47. Reproductive effort* of O. irroratus, R. pumilio and P. natalensis in the areas indicated. T = Transvaal highveld; F = Fish River valley; N = Natal midlands. 1 = Meester & Hallett (1970); 2 = Davis (1973); 3 = Brooks (1974); 4 = Coetzee (1975); 5 = Baker & Meester (1977); 6 = Perrin (1980b); 7 = Davis & Meester (1981).

SPECIES	LOCALITY	N	W_w	m	R_e	SOURCE
O. irroratus	T	2.33	30.1	140	0.74	2, 7
O. irroratus	F	1.48	22.0	109.5	0.44	6
R. pumilio	T	5.90	10.4	45.6	1.95	3
R. pumilio	F	4.90	11.0	39.9	1.86	6
P. natalensis	N	11.27	12.2	41.8	4.48	5
P. natalensis	**	10.00	11.0	50.0	3.21	1, 4

* $R_e = N W_w^{0.75} (m^{0.75}) - 1$

** possible general species mean

overestimate), the result is R_e = 3.91. The R_e referred to as a possible general species mean for P. natalensis (Table 47) was calculated using the general mean litter size of 10 suggested by Coetzee (1975) in conjunction with a mass at weaning of 11g (Meester & Hallett 1970) and a probably inflated female mass of 50g. It is apparent from the R_e values in Table 47 that reproductive effort per pregnancy in P. natalensis is considerably higher (probably more than twice as high) than in R. pumilio, which in turn invests as much as four times as much energy per pregnancy as O. irroratus (Perrin 1980b). However, Perrin (1980b) draws attention to the fact that differences in the seasonality of breeding in O. irroratus and R. pumilio (below) may approximately halve the annual disparity in reproductive effort between these species.

Perrin (1980b) suggests that the reproductive effort of male O. irroratus and R. pumilio may be similar. Very little is known of reproduction in O. irroratus, but the amount of energy expended in courtship by male R. pumilio seemed far greater than in P. natalensis (sections 4.4.3, 5.3.2.1). In view of the modes of dispersion of these two species (section 5.4.2) there is no reason to doubt that the same disparity obtains in free-living males.

The majority of Southern African rodents for which records exist (Roberts 1951; De Graaff 1981) display distinct reproductive seasonality, breeding during the wetter months, at least in the summer rainfall region, and undergoing a period of reproductive quiescence in winter. O. irroratus, R. pumilio and P. natalensis all have about a nine-month breeding season (September - May) on the Transvaal highveld (De Wit 1972; Davis 1973; Brooks 1974; Davis & Meester 1981), although Coetzee (1965) noted greatly reduced winter breeding in a P. natalensis population at Roodepoort, rather

than an absolute lack of breeding. In the S.W. Cape (Cape Flats and elsewhere) R. pumilio has retained the seasonal pattern of reproduction described above, presumably because food supply is greater during the warmer months than in winter (David 1980), despite the almost total lack of rainfall during the period October - March. R. pumilio breeds intermittently in the Fish River valley, with pregnancies occurring in spring and autumn, and not in winter or mid-summer; in contrast O. irroratus breeds throughout the year, with 50-100% of adult females being pregnant in all months (Perrin 1980b). In Perrin's study, breeding in R. pumilio, but not in O. irroratus, was positively correlated with rainfall of two (pregnancy) or three (recruitment) months previously. Hence, it appears that a tendency toward semelparity is typical only of R. pumilio, while in certain circumstances both O. irroratus (Perrin 1980b) and P. natalensis (Coetzee 1965) may tend toward iteroparity.

Perrin (1980b) appears to regard continuous breeding in O. irroratus as typical of the species, and cites FitzSimons (1920) as stating that breeding in this species occurs year-round. However, FitzSimons also said that O. irroratus produces 5-12 young/litter, which is clearly incorrect, so that he was doubtless referring to some other species; this makes his reference to year-round breeding highly suspect. Perrin (1980b) also uses as supporting evidence the fact that the central African O. tropicalis, which he regards as synonymous with O. irroratus, is a continuous breeder (Dieterlen 1968). However, irroratus and tropicalis are unlikely to be synonyms (section 1.2.2), and even if they were, continuous breeding in the tropics could not be taken to indicate that the same pattern would occur in the more temperate Southern Africa (Pianka 1970).

The most likely explanation for the different patterns of reproductive activity observed in O. irroratus by Davis (1973) and Perrin (1980b) is that this species has adapted its breeding to local environmental conditions. An obvious and probably important difference (as far as breeding in O. irroratus is concerned) between the Transvaal highveld and Fish River valley environments lies in the distribution of mean monthly rainfall in the two areas. During the months June - August, when O. irroratus did not breed in Davis' (1973) study area, rainfall is at its lowest in that region, ranging from 11mm in June to an insignificant 4mm in August (Davis 1973; Davis & Meester 1981). In all of these months, mean rainfall is higher in the Fish River valley (approximately 24mm in June, 16mm in July and 56mm in August; Perrin 1980b) than on the Transvaal highveld, and is apparently high enough to maintain at a more or less constant level throughout the year the quality of the plant material on which O. irroratus feeds (Perrin 1980a). On the Transvaal highveld, rainfall was cited together with photoperiod, temperature and food as potentially controlling reproductive activity in O. irroratus (Davis 1973; Davis & Meester 1981), although the occurrence of continuous breeding in the Fish River valley appears to cast doubt on the idea that photoperiod influences breeding in this species.

Fertility, the actual level of reproductive performance of a population, must be distinguished from fecundity, the potential level of performance under ideal conditions (Krebs 1978). Fertility may be measured as the product of litter size and the number of litters produced over a given time. Table 48 gives the estimated annual fertility of O. irroratus, R. pumilio and P. natalensis from data available in the literature. The fertility value of 24 ascribed to R. pumilio (Table 48) was calculated using a mean number of four litters, which is probably more realistic (Powell

Table 48. Fertility of O. irroratus, R. pumilio and P. natalensis in the areas indicated, measured as the product of mean litter size and mean annual number of litters. T = Transvaal highveld; F = Fish River valley; C = Cape Flats; 1 = Coetzee (1965); 2 = De Wit (1972); 3 = Davis (1973); 4 = Brooks (1974); 5 = David (1980); 6 = Perrin (1980b); 7 = Davis & Meester (1981).

SPECIES	LOCALITY	$\bar{X}$ LITTER SIZE	NO. LITTERS	FERTILITY (young p.a.)	SOURCE
O. irroratus	T	2.33	4 or 5	9 - 12	3, 7
O. irroratus	F	1.48	7	10	6
R. pumilio	T	5.90	4*	24	4
R. pumilio	F	4.91	3	15	6
R. pumilio	C	4.92	2	10	5
P. natalensis	T	9.22	4	37	1
P. natalensis	T	8.00	3*	24	2

* extrapolated values; see text

1925) than the maximum possible number (six) given by Brooks. The value of three litters used to calculate the fertility of 24 in P. natalensis was extrapolated from the length of the breeding season and short lifespan of this species (above) in De Wit's (1972) study area. Two trends are evident in Table 48, namely that the fertility of R. pumilio and P. natalensis, but not of O. irroratus, appears regionally variable, and that there is a gradation in fertility: P. natalensis > R. pumilio > O. irroratus.

Survival to reproductive age is a vital component of fitness, and relative development of parental care, even if only to weaning as in most rodents, is an important determinant of overall reproductive capacity. The significance of well developed parental care in O. irroratus was discussed by Davis (1973) and in more detail by Davis & Meester (1981). These authors concluded that while litter size is low (above), good survival of young would permit high overall reproductive potential in this species. Three interrelated adaptations which appear to potentially increase survival of young (by reducing susceptibility to predation) are here distinguished, and their relative development in the three species described (Table 49).

A number of parameters of parental care included in Table 49 require comment. During the gestation period, young experience not only extreme environmental stability but also a high degree of protection (Millar 1977), particularly against predation. (There is also an advantage to the mother in a prolonged gestation period, namely that the energy cost of pregnancy is lower than that of lactation; Millar 1977.) Young which are large in size and precocial at birth, and which rapidly develop efficient locomotion and wean early, are presumably less vulnerable to predation and other mortality factors than are altricial young (Millar 1977; Davis & Meester

Table 49. Parental care in O. irroratus, R. pumilio and P. natalensis. 1 = Meester & Hallett (1970); 2 = Davis (1973); 3 = Brooks (1974); 4 = Coetzee (1975); 5 = Baker & Meester (1977); 6 = Davis & Meester (1981); 7 = present study (section 5.4.2.2).

SPECIES	CONDITION OF YOUNG AT BIRTH	RATE OF DEVELOPMENT	BEHAVIOURAL FACTORS	SOURCE
O. irroratus	Large ($\bar{X}$ = 12.5g) and precocial (gestation period 40 days or more) with incisors erupted.	Rapid (locomotion efficient by day 5; weaning by day 13).	Nipple-clinging characteristic. Short distance of dispersal.	2, 6
R. pumilio	Small ($\bar{X}$ = 2.5g) and altricial (gestation period 25 days).	Less rapid than O. irroratus but more rapid than P. natalensis (locomotion efficient by day 10; weaning by day 14).	Possible two-phase dispersal from maternal territory.	1, 3, 7
P. natalensis	Small ($\bar{X}$ = 2.2g) and altricial (gestation period 23 days).	Slower than R. pumilio (locomotion efficient by day 12; weaning by day 20).	Parturition in underground burrow.	1, 4, 5

1981). The phenomenon of nipple-clinging in O. irroratus (Table 49) is regarded as reducing mortality in this species (Davis 1973; Davis & Meester 1981), and judging by the small litter sizes of species in which nipple-clinging occurs (Davis 1963; Meester & Hallett 1970) this may generally be the case, although not necessarily so (Millar 1977). Establishment of some young within or in the vicinity of the mother's territory in O. irroratus, and possible two-phase dispersal in R. pumilio (Table 49) appear to represent extensions of maternal care beyond weaning, although in these instances reduction of intraspecific competition may be more important than reduction of predation (sections 5.4.2.1, 5.4.2.2).

The content of Table 49 and of the above paragraph suggests that there is a gradation in the degree of parental care, and consequently of survival of young, in the three species: O. irroratus > R. pumilio > P. natalensis. However, the apparent disadvantage of P. natalensis in this respect may be partially offset by the fact that the young are produced in an underground burrow, the more or less stable microclimate of which would tend to increase juvenile survival relative to that in O. irroratus and R. pumilio, which generally nest on the surface (section 1.2.6).

7.2.4. Population density

Few studies have been undertaken which permit comparison of population density in Southern African rodents. Concurrent studies on O. irroratus and R. pumilio on the Transvaal highveld (Davis 1973; Brooks 1974) showed that there were year-to-year changes (over a 27-month period) in the proportions of the two species in their catches. During the period March-November 1970 R. pumilio was numerically the more important; thereafter (December 1970-May 1972) numbers of O. irroratus were greater than those of

R. pumilio. In the Fish River valley Perrin (1980b) observed similar variability in relative numerical importance of these two species over an 18-month period, with R. pumilio initially predominant (July-December 1976), and thereafter (January-December 1977) O. irroratus was more numerous in most months; in terms of biomass O. irroratus was more important than R. pumilio in all but three months (July-September 1976). In De Wit's (1972) 16-month (February 1970-July 1971) Transvaal highveld study P. natalensis was the most abundant species in all months other than January-March 1971. R. pumilio was present in small numbers throughout the study, but was numerically unimportant. In the present study the limited amount of trapping undertaken (section 3.2.1.2) suggested that generally speaking R. pumilio was more abundant than O. irroratus at the Dargle grassland area, and that P. natalensis was more numerous than O. irroratus and R. pumilio at the remaining sites (section 3.3.1).

All three species display distinct seasonal variation in abundance, although the occurrence of density peaks seems to vary from area to area. On the Transvaal highveld densities of both O. irroratus and R. pumilio peaked in late autumn and early winter (May-June; Davis 1973; Brooks 1974). On the Cape Flats peak densities of R. pumilio generally occur in late summer and autumn (February-May; David 1980). The early peak in R. pumilio numbers in the S.W. Cape, which was fairly consistent over a five-year period (1972-1977; David 1980), is probably associated with the intensity of the drought prior to the commencement of the rainy season. Perrin's (1980b) Fish River valley study showed fluctuations in density of both O. irroratus and R. pumilio to be less regular than in the areas referred to above, probably because of the unpredictability of rainfall in the E. Cape. However, population densities of O. irroratus were generally less variable than those of R. pumilio (Perrin 1980b).

Peak densities of P. natalensis generally occur toward the end of autumn and beginning of winter, both on the Transvaal highveld (Coetzee 1965) and elsewhere (Coetzee 1975). Reproductive activity in P. natalensis is strongly influenced by rainfall (e.g. Coetzee 1975), and the abnormal autumn decline which occurred during 1970 in De Wit's (1972) study was the result of dry conditions at that time.

While all three species are clearly subject to variation in population density, O. irroratus may be generally less susceptible to such fluctuations than is R. pumilio (Perrin 1980b), which in turn probably experiences more stable population densities than P. natalensis. The latter conclusion is based on reports of periodic irruptions and subsequent crashes in density of P. natalensis (Veenstra 1958; van der Merwe & Keogh 1970, in Cilliers 1972; Choate 1972; Kingdon 1974; Coetzee 1975). While irruptions of P. natalensis occur unpredictably as a result of unusual circumstances (probably climatic/vegetational; J. Meester In litt.), and are superimposed on the annual cycle referred to above, they nonetheless serve to illustrate the extreme variability in population density of this species. There have been no reports of irruptions of either of the other species, and David (1980) specifically noted the absence of evidence for long-term cycles in R. pumilio in his five-year study on the Cape Flats.

7.2.5. Social organization

Happold (1973) considered the adaptive significance of the social systems of several species of conilurine rodents in terms of the carrying capacities of the habitats in which they occurred. She concluded that cohesive and dispersed social systems are r- and K-strategies respectively, and although factors other than the carrying capacity of the habitat may

influence social organization, studies on other taxa were cited as supporting her conclusions (Australian parrots - Brereton 1971, and African bee-eaters - Fry 1972, in Happold 1973). However, the existence of coloniality in K-selected New World jays (Brown 1974; see section 6.3) shows that there is not a universal correlation between well and poorly developed sociality and r- and K-selection respectively, although the occurrence of such a correlation has not, to my knowledge, been refuted in the literature pertaining to small mammals.

The social systems of O. irroratus (dispersed; section 5.4.2.1) and P. natalensis (cohesive; section 5.4.2.3) are here regarded as correlates of K- and r-selection respectively. The tendency for aggregation in non-breeding R. pumilio, in which territoriality is well represented during the breeding season (section 5.4.2.2), suggests that in terms of its social organization it would fall between O. irroratus and P. natalensis on an r-K continuum.

7.2.6. Interspecific competition

Little is known of the competitive abilities of the three species in relation to one another, or to other small mammal species. Competition for food between O. irroratus and R. pumilio in the Fish River valley may be minimal (Perrin 1980a), although competition for space on the Transvaal highveld appears to result in R. pumilio giving way to O. irroratus (Brooks 1974). The upright posture and "chitting", prominent in the O. irroratus agonistic repertoire (section 4.3.3), are employed by this species in situations of interspecific confrontation in the laboratory, and cause the withdrawal of both R. pumilio and P. natalensis (Pers. obs.). P. natalensis is known to give way to both O. irroratus and R. pumilio in

grassland recovering after fire (e.g. Natal midlands; Meester et al 1979), and to Rattus rattus in areas suitable for habitation by this mainly commensal species (Kingdon 1974; Coetzee 1975). P. natalensis flourishes in disturbed areas (section 1.2.5), but low numbers of O. irroratus and R. pumilio in such habitats is probably the result of factors (e.g. cover; section 3.4.2) other than competition with pioneer rodent species. Thus, there is probably a general gradation in interspecific competitive abilities: O. irroratus > R. pumilio > P. natalensis.

7.3. r- and K-selection in O. irroratus, R. pumilio and P. natalensis

In terms of all of the correlates of r- and K-selection listed in section 7.2, O. irroratus approaches the K-endpoint more closely than either R. pumilio or P. natalensis (sections 7.2.1 - 7.2.6), except that there is an apparent tendency toward iteroparity in P. natalensis (section 7.2.3), which is characteristic of K-selected species. In terms of all correlates (section 7.2) other than body size (which is similar in R. pumilio and P. natalensis; section 7.2.2) and breeding seasonality (where P. natalensis tends toward iteroparity while R. pumilio does not; section 7.2.3) P. natalensis approaches the r-endpoint more closely than R. pumilio (sections 7.2.1 - 7.2.6).

It is clear from the above that compared with the other species considered here O. irroratus is relatively K-selected and P. natalensis relatively r-selected, with R. pumilio falling between these two extremes.

Perrin (1980b) is clearly correct in describing O. irroratus as relatively K-selected. Davis & Meester (1981) suggested that this species probably occupies an intermediate position in relation to r and K, citing

a number of characteristics as indicating K-selection (large body size, high longevity, small litter size, prolonged breeding season, well developed parental care and high survival rate of young), but stressing the effects of environmental instability on food supply and population size of O. irroratus as favouring r-selection in this species. However, Davis & Meester (1981) refer to the stabilizing influence of dense vegetation on microclimate in the mesic habitats favoured by O. irroratus, and such areas are probably better thought of as stable rather than unstable (section 3.4.4.2). In addition, Pianka (1970) noted that terrestrial vertebrates in general appear relatively K-selected, and all three species being considered here are doubtless more nearly K- than r-selected, but with O. irroratus most closely approaching the K-endpoint.

CONCLUSION

This study has added to a growing body of information on the relationship between rodent social organization and ecology. Socio-ecological trends similar to those observed in the conilurine rodents (Happold 1973, 1976) and marmots Marmota (Barash 1974), on which work the present study was largely based, have been recorded in the species considered here, namely that stable and unstable environments appear to select for dispersed and aggregated social systems respectively. However, as pointed out in section 6.3, this type of correlation is by no means universal among animal species, and it is clear that further information (see below) is required before a general socio-ecological hypothesis can be proposed (Barash 1977).

Conclusions in respect of availability of resources to Otomys irroratus, Rhabdomys pumilio and Praomys natalensis in their preferred habitats (section 3.4.4.2) would have been strengthened by detailed information regarding seasonal and long-term variation in the carrying capacity of different habitat types for these species. Newsome (1967) described a method whereby the food supply of free-living Mus musculus was measured. By placing individual mice in open-bottomed containers of known size in the field and weighing the animals at regular intervals, he ascertained for how long they could maintain mass on the food naturally present in that area of habitat. Adaptation of this method to local conditions would possibly provide a measure of the carrying capacity of different habitat types for Southern African rodents. (I attempted to measure the food supply of O. irroratus and R. pumilio at the Dargle grassland study area using Newsome's method, but the results were too variable to be of use; this was probably because the 0.5m^2 enclosures used were too small to contain a representative area of habitat, and their small size led to some

animals expending considerable energy, hence losing mass, in attempting to escape; Willan Unpubl.)

Previous work on socio-ecology has often concentrated on species which belong to the same genus (e.g. Marmota; Barash 1974; Anderson et al 1976; Armitage 1977) or are otherwise closely related and have a clear monophyletic origin (e.g. conilurine rodents; Happold 1973, 1976). Although valuable comparative work has been done on species which are not closely related (e.g. large herbivores; Jarman 1974), Barash (1977) suggests that comparative socio-ecological studies at the intrageneric or intraspecific (i.e. subspecies) levels are the most valuable. A number of potentially valuable investigations into the social ecology of Southern African rodents have suggested themselves as a result of the present study. I have recently started a study on the social ecology of O. unisulcatus, which occurs in drier, less stable habitats, and is thus predicted to be considerably more sociable than O. irroratus. Other species of Otomys will be investigated in due course, for example saundersae and sloggetti, which occur in unstable montane habitats and like unisulcatus are probably comparatively sociable, and angoniensis, a grassland species which is probably more sociable than irroratus, but less so than the other species referred to above. An interesting and informative study could be undertaken on relative sociability of R. pumilio from different parts of its range, for example the S.W. Arid where it is comparatively sociable (Nel 1975) and Zimbabwe where males appear to be highly territorial (Choate 1972). Quantitative confirmation of these observations would provide strong support for the correlation referred to above, relating low sociability to high environmental stability, and vice versa. Similarly, a comparison of the social organization of O. irroratus adapted to harsher environmental conditions than obtaining in the Natal midlands would be of interest. A

small number of observations on dyadic interaction between captive O. irroratus from S.W. Cape montane fynbos (Pers. obs.) suggested that this species is less overtly aggressive in that region than in the Natal midlands.

Attempts were made in the present study to observe social interaction in the field, but due to the density of vegetative cover this was generally unsuccessful (section 1.1). However, it is possible to observe free-living animals of all three species in areas where vegetation is less dense than in the Natal midlands (Pers. obs.), and such observation would provide a useful supplement to information at present available. Observation at feeding stations of previously marked animals (e.g. by fur-clipping or using ear tags) would maximize the useful data obtained in this type of study. Radio-tracking has not to my knowledge been used in work on African terrestrial small mammals, although bats have been studied in this way (L.R. Wingate Pers. comm.). Use of this technique would provide more precise information on patterns of movement, habitat utilization and social organization of free-living small mammals than is obtained by trapping.

Following Stearns (1976), Perrin (1980b) has emphasized the need to consider life-history tactics in terms of hypotheses (e.g. bet-hedging) which offer alternatives to the environmental stability/instability explanation of r-K theory, which he regards as simplistic. However, consideration of the life-histories of O. irroratus, R. pumilio and P. natalensis in terms of bet-hedging would require information which is not at present available on these species. The bet-hedging hypothesis predicts that in unstable environments high juvenile mortality results in selection for increased longevity and reduced reproductive effort, with

the opposite effects in the case of high adult mortality (section 7.1). Predation is generally the most important mortality factor in rodents (Blair 1948), but the effects of predation on the three species considered here have not been carefully investigated.

Prior to any attempt to interpret the life histories of the three species in terms of bet-hedging, attention should be given to at least the following important questions in respect of mortality in the three species: 1. The comparative importance of predation and other mortality factors in determining adult and juvenile mortality; 2. The effect of differences in patterns of diel activity, nest-site selection and environmental variables (e.g. cover) on the vulnerability of adults to predation (O. irroratus and R. pumilio display wider ranges of diel activity and generally nest on the surface, and are thus exposed to a greater variety of predators than is P. natalensis, which is strictly nocturnal and nests in a burrow, the entrance to which may be plugged during the day - Pers. obs.; O. irroratus prefers high vegetative cover which may make it less accessible to predators than are the other two species, but this may be counteracted by the possibility that predators are generally more abundant in mesic than in more xeric habitats); 3. The effect of differences in nest-sites and parental care, especially nipple-dragging in O. irroratus, on survival of young (parental care in P. natalensis appears less well developed than in the other two species, but birth of the young in a burrow may provide considerable protection against predation; moreover, the existence of food-caching in P. natalensis - Veenstra 1958; Cilliers 1972 - and the fact that heavily pregnant or lactating females rarely leave the nest - Cilliers 1972 - suggests that survival of young may be high); 4. The effect of pregnancy, when females are at their most vulnerable, on survival (at birth, a P. natalensis litter may weigh 40-50% of the mother's mass, suggesting high vulnerability to predation compared to O. irroratus and R. pumilio, where

the litter may weigh 20% or less of the mother's mass; however, restriction to the nest may greatly reduce the danger of predation to heavily pregnant P. natalensis females).

SUMMARY

The study aimed to describe the socio-ecological niches of Otomys irroratus, Rhabdomys pumilio and Praomys natalensis in the Natal midlands. To achieve this objective, it was necessary to investigate various aspects of the ecology of the three species which were poorly understood, and to undertake comparative studies of their social behaviour and social organization.

Field studies (habitat and trapping) were undertaken during the period September 1976-July 1977 at three sites (two at Dargle State Forest, and one at Darvill Sewage Works, Pietermaritzburg) which differed in terms of abiotic and biotic characteristics. These studies aimed to distinguish the primary habitat preferences, as determined by water availability (i.e. distribution in relation to distance from water, substrate moisture, and cover density), of the three species, which are sympatric in many parts of Southern Africa, and to investigate the modes of dispersion of free-living populations. Experimental and observational studies were undertaken during the period January 1976-May 1978. Captive studies on responses to substrate moisture, cover availability, swimming ability and the effects of food and water deprivation provided data supporting and extending information obtained in the field and available in the literature. Observational studies on the interaction of conspecific dyads permitted comparative analyses of social behaviour and social organization in captivity, and provided a basis for interpretation of trap-revealed dyadic association in the field.

The position of the three species relative to one another on a mesic-xeric continuum, defined as having a range of +1 (100% mesophilous)

to -1 (100% xerophilous), was ascertained using data for 21 categories of information obtained in the field or laboratory. On this continuum, O. irroratus obtained a score of +0.46, indicating a mesophilous tendency relative to the other two species; R. pumilio scored -0.05, suggesting a slight xerophilous tendency, and P. natalensis a neutral (i.e. neither mesophilous nor xerophilous) 0.00. However, weighting was not employed in the scoring system, and the importance of efficient utilization by R. pumilio of highly hydrated foods (e.g. insects) was probably underestimated. Hence, R. pumilio is probably more nearly xerically adapted (relative to the other two species) than indicated by its small negative score, above. Apparently overriding the influence of water availability on the habitat preferences of P. natalensis, this species favours disturbed environments.

The habitats preferred by the three species in the Natal midlands were described as follows: O. irroratus - mesic areas with good vegetative cover; resource availability is variable in space (i.e. small areas of optimum habitat), but within these areas is high and stable in time; R. pumilio - drier areas with less dense vegetation, and with resource availability less variable in space (i.e. large areas of optimum habitat), but less stable in time (i.e. seasonally ephemeral) than in the mesic habitats favoured by O. irroratus; P. natalensis - disturbed habitats; availability of such habitats, and hence of resources, is highly variable in space (i.e. resulting from possibly localized chance disturbance of the environment) and time (i.e. dependent on the rate of ecological succession).

Social behaviour of approximately 50 dyads of each species was qualitatively studied in observation cages for about 400h/species; records were kept of the structure and function of behavioural postures, sequences

and responses, and of potentially social acts (i.e. sound production within the range of human hearing, and marking behaviour).

Communication in O. irroratus appeared to be dominated by low frequency vocal signals, although visual signals which involved large-scale changes in posture were also well developed. R. pumilio also emphasized visual communication, but its signals were subtle, mainly involving small changes in the disposition of various external organs such as the eyes and ear pinnae. P. natalensis appeared to rely largely on olfactory communication.

O. irroratus was the most overtly aggressive of the three species, but agonism was ritualized, and damaging fights were rare. R. pumilio was less overtly aggressive than O. irroratus, but agonism tended to be direct, with non-aggressors tending to flee from rather than submit to aggressors. Aggression was poorly developed and ritualized in P. natalensis.

O. irroratus does not breed in captivity, but sexual behaviour was observed in the other two species. In R. pumilio, energy expenditure in courtship was high, but mating occurred more rapidly (at times within 15 minutes of animals first meeting) than in P. natalensis, where courtship continued intermittently for at least two days before mating was achieved. Ovulation appears to be reflex in R. pumilio and spontaneous in P. natalensis.

A quantitative study of dyadic interaction in the three species was undertaken in the laboratory. Four dyads of each of the 10 possible combinations of four castes (scrotal and non-scrotal males and perforate and imperforate females) were studied for 5h/dyad (one hour/day for five

days). Trapping data were used to calculate indices of association for free-living dyads; 21 dyadic combinations were recognized for each species, and comprised all possible combinations of the four castes listed above, together with sub-adults and juveniles. Animals of the same species were regarded as associating together in the field if they were captured at the same or adjoining trap-stations within 48h of one another.

The results of the field and laboratory studies, together with information available in the literature, permitted the following descriptions of the social systems of the three species: O. irroratus - animals live in close spatial association (i.e. the system is cohesive in space), but the probable existence of temporal territoriality in this species suggests that individuals may seldom meet face to face (i.e. the system is dispersed in time); in addition, breeding females are intrasexually territorial, and hierarchical relationships exist among males; R. pumilio - during the breeding season the system is based on female intrasexual territoriality and male hierarchical ranking; there is a tendency for aggregation in mesic refuge habitats in the winter non-breeding period; P. natalensis - the colonial social organization is based on dominance hierarchies, the structure of which depends on demographic factors; alpha animals of both sexes probably maintain small territories in the vicinity of their nests.

Dispersal in O. irroratus probably occurs when the young are about 40 days old, coinciding with late pregnancy in the mother, assuming fertilization during a post-partum oestrus. Distance of dispersal is short in this species, with young apparently attempting to establish home-ranges overlapping that of the mother. Young R. pumilio probably disperse to the periphery of the breeding population, but a two-phase system of dispersal was proposed for this species in which young of a first litter leave the maternal nest when a second is born, but remain

within the mother's territory until the birth of a third litter. Weaned P. natalensis young probably remain within the parent population, with dispersal mainly by subordinate adult males.

O. irroratus and R. pumilio probably mate promiscuously, although locally dominant males would achieve higher fertilization rates than subordinates. In P. natalensis, members of an alpha group comprising males and females appear to account for the bulk of reproductive activity. This species may tend toward monogamy, particularly at low population densities.

In general, the social behaviour and social organization of the three species are clearly adapted to their preferred habitats and other aspects of their ecology.

O. irroratus is very vocal within the range of human hearing; its use of loud vocalizations is seen as informing conspecifics of their precise location in relation to one another even in densely vegetated habitats. Such information would tend to reduce levels of direct conflict in this aggressive species, and would be an important mechanism whereby temporal territoriality was achieved. The use by O. irroratus of large-scale movements as visual signals is probably an adaptation to communication at low light intensities (i.e. this species is largely crepuscular, and prefers densely vegetated habitats in which little light penetrates to ground level). Subtle visual signals such as those used by R. pumilio would not be easily visible at low light intensities. Ritualized aggression in O. irroratus, together with temporal territoriality, appear to be adaptations which would permit high densities of this species to occupy small areas of habitat in which the carrying capacity is perennially high. Intrasexual territoriality in females may have evolved to provide

dispersing young with space for establishment of a home-range within a potentially limited area of prime habitat.

R. pumilio appears to be largely dependent on visual communication; its use of subtle visual signals, which are emphasized by morphological characters (e.g. bands of yellow hairs above and below the eyes), is possible because it is usually active under conditions of high light intensity (i.e. it is diurnal, and prefers areas of less dense vegetative cover than O. irroratus). Direct (i.e. unritualized) aggression in R. pumilio probably acts as a spacing mechanism, reflecting the large areas of suitable habitat available to this species. The essentially dispersed (rather than aggregated) social organization of R. pumilio is apparently adapted to the exploitation of resources which are more or less evenly distributed through large areas of habitat, and generally less abundant than those utilized by O. irroratus. Female intrasexual territoriality and two-phase dispersal of young are apparently adaptations to safeguard juveniles against conspecific female aggression. Winter aggregation of R. pumilio in mesic refuge habitats apparently reflects the seasonality of resources available to this species in drier areas. High energy investment in courtship by male R. pumilio and reflex ovulation in females would maximize fertilization rates in a social system where animals are not in frequent contact with one another.

P. natalensis is nocturnal, and as such appears to emphasize olfactory communication, although ultrasonic signalling is probably also important in this species. In addition to the constraints placed by low light availability on communication (e.g. visual signals may be invisible in the dark), odours may be important in maintaining group cohesion in P. natalensis, as in other highly sociable rodents such as Rattus norvegicus.

Low levels of agonistic interaction in P. natalensis (and conversely, higher levels of amicable behaviour than in the other two species), together with ritualization of aggression, doubtless also serve to maintain the cohesive social group. Coloniality and delayed dispersal in P. natalensis are seen as permitting high population densities of this species to exploit temporarily abundant resources in transitory disturbed habitats. Small rodents adapted to desert environments are generally also subject to unpredictable availability of resources, and are often colonial. (Arid-zone R. pumilio are apparently more sociable than populations in wetter areas.) Low intensity courtship and spontaneous ovulation in P. natalensis are possible because of the ready availability of potential mates within the highly aggregated society.

The life history tactics of the three species were interpreted in terms of the theory of r- and K-selection. Thirteen correlates of r- and K-selection were considered, and the positions of the three species on an r-K continuum ascertained. In terms of all correlates, O. irroratus approaches the K-endpoint more closely than the other two species, except that P. natalensis tends toward iteroparity in some circumstances, which is a K-selected character. P. natalensis approaches the r-endpoint more closely than R. pumilio in respect of all correlates other than body size (which is similar in the two species) and breeding seasonality (with P. natalensis tending toward iteroparity, and R. pumilio toward semelparity). Hence, O. irroratus is relatively K-selected compared with the other two species, and P. natalensis is relatively r-selected, with R. pumilio falling between the two extremes.

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Appendix 1

The Effects of Fire Regime on Small Mammals in S.W. Cape Montane Fynbos (Cape Macchia)[1]

K. Willan and R. C. Bigalke[2]

Abstract: Small mammal species richness, abundance and biomass were determined in representative S.W. Cape montane fynbos habitats of various post-fire ages, and in riverine and rocky outcrop habitats respectively too wet and too poorly vegetated to burn. In fynbos the parameters measured displayed bimodal distributions, with early (2,4 years) and late (38 years) peaks and intervening troughs (10-14 years). Correlations with plant succession are discussed. In comparison with other ecotypes, recolonisation of burns by small mammals occurs more slowly in fynbos. Species richness, abundance and biomass of small mammals was consistently higher in riverine habitats than on rocky outcrops. The former may serve as major sources of recolonisation after fire.

There is no published information on the effects of fire on small mammals in fynbos although ecosystem dynamics cannot be fully understood without knowledge of these effects. Three studies have been undertaken (Taes 1972; Lewis In prep; Bigalke and Pepler Unpubl.), and Bond and others (1980) commented on potential fire effects in the Southern Cape mountains. The present pilot study took place in S.W. Cape montane fynbos preparatory to intensive investigation of the effects of fire regime on non-fossorial small mammals. The project has been temporarily suspended, and preliminary conclusions are presented here.

METHODS

Trapping was undertaken from August to November 1979 at selected sites in three Department of Forestry mountain catchment reserves, Jonkershoek (33°59'S, 18°59'E; ± 400m), Hemmershoek (33°48'S, 19°02'E; ± 800m) and Lebanon (34°09'S, 19°09'E; ± 900m). 34 sites were trapped, 22 in representative fynbos and 6 each in riverine habitats and rocky outcrops. The riverine and rocky outcrop habitats appeared respectively too wet and too poorly vegetated to burn; they were sampled to ascertain their potential as refuge habitats after fire (Vesey-Fitzgerald 1966), when the surrounding vegetation had been destroyed. The fynbos study areas were selected on the basis of the post-fire age of the vegetation (2, 4, 10, 14 and 38 years old). The effects of variables other than post-fire age were largely neutralised by sampling a number of sites in each area which were analogous to sites in other areas. In this way area effects resulting from differences in aspect, slope, rockiness and proximity to surface water were more or less eliminated. Unavoidable variation occurred in season, altitude and vegetation floristics and physiognomy. In the 2-14-year-old areas, trapping sites included vegetation dominated respectively by Proteaceae, Ericaceae and Restionaceae, but this was impossible in the 38-year-old area where Protea repens and Widdringtonia nodiflora were dominant, although the proteas were dying out, leaving much dead wood on the ground and permitting recolonisation by ericas and restios. The most important feature of these habitats in relation to the study objectives was that while the young (2- and 4-year-old) and old (38-year-old) vegetation could be regarded as productive (i.e. actively growing, the latter due to recolonisation by ericas and restios), the 10- and 14-year-old vegetation was clearly moribund, and floristic and physiognomic diversity was consistently lower than in either the young or senescent habitats. In an attempt to obtain an overview of small mammal preferances for these habitats, data are combined where areas of the same general type (i.e. riverine or rocky outcrop habitats, or ones of the same post-fire age) were sampled in different catchments.

A summary of sampling effort in each type of habitat is given in Table 1. In the fynbos and mesic refuge habitats, trapping took place on transect lines of variable length (11-20 stations, depending on local conditions), with 15m between stations. Trapping on rocky outcrops was more or less ad libitum, with traps set at places where they seemed most likely to make a catch. 2 live-traps were used at every station, 1 Sherman 230 x 80 x 90 mm and 1 PVC tunnel trap 250 x 65 x 78 mm (after Willan 1979). Traps were set within 1m of station markers abutting small mammal runways if present, and checked morning and evening for a total of 4 days and nights. Bait was a mixture of rolled oats, raisins and sunflower oil; pre-baiting was not employed. Animals were released at the point of capture after species and mass

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Table 1--Sampling effort (station-nights) in various S.W. Cape fynbos habitats. The number of sites sampled within each area is given in brackets.

Study areas	Month sampled	Montane fynbos - age in years					Mesic refuges	Rocky outcrops	Totals
		2	4	10	14	38			
Vemmershoek	August	130(2)			180(3)		180(3)	200(4)	690(12)
Lebanon	September			300(6)			40(1)	100(2)	440 (9)
Jonkershoek	November	80(2)	430(6)			180(3)	100(2)		790(13)
Totals		210(4)	430(6)	300(6)	180(3)	180(3)	320(6)	300(6)	1920(34)

had been recorded and to avoid interfering with proposed trap-mark-release studies, they were marked only by clipping the fur. Results are interpreted as indices of relative abundance, expressed as trap-success/station-night of effort, where "station-night" described trapping for a 24-hour period with two traps/station. Data of this type may be expressed in terms of "trap-success" (e.g. Meester and others 1979; Mentis and Rowe-Rowe 1979), but in the present report this would have been misleading since it was uncommon (less than 3 percent of captures) for more than one animal to be trapped at the same station at the same time. Relative biomass was calculated as total biomass divided by sampling effort, hence as g/station-night.

Otomys spp. are difficult to distinguish in the field, and while J. Meester (pers. comm.) identified as O. irroratus all specimens in a small voucher series from the 3 catchments, O. laminatus and O. saundersae also occur in fynbos (Davis 1974), with O. saundersae previously recorded from Jonkershoek (Stewart 1972). The possible irroratus/laminatus/saundersae complex present in the sample is referred to as Otomys throughout, although the great majority were probably O. irroratus. This approach appears reasonable in view of the similarity in habits of Otomys spp. (Roberts 1951; Kingdon 1974).

RESULTS

A total of 460 rodents and insectivores, representing 12 taxa, were captured during the study (table 2), 83 percent of which were Aethomys namaquensis, Otomys spp., Rhabdomys pumilio and Mystromys albicaudatus.

Species richness (fig. 1) was highest in the riverine habitats, where all but one species (Elephantulus edwardii) were present, and lowest on rocky outcrops and in 14-year-old fynbos. In the fynbos habitats it was variable, with early (4-year) and late (38-year) peaks, and an intervening (10-and 14-year) trough.

Relative abundance (fig. 2) was highest in the riverine habitats, and lowest on rocky outcrops. In the fynbos habitats, relative abundance displayed early and late peaks, with an intervening trough, but within the overall bimodality considerable species-specific variation existed. The most important characteristics of the distribution illustrated in figure 2 are as follows:

1--Abundance of Aethomys namaquensis, Mus minutoides and Dendromus melanotis declined with increasing age of the vegetation, and D. mesomelas replaced D. melanotis as the vegetation became more rank.

2--Otomys spp. were initially (2 years) poorly represented, but thereafter maintained an important presence.

3--Rhabdomys pumilio was most abundant in young (2-and 4-year-old) and old fynbos, but declined in middle age; ad libitum trapping in an area of younger fynbos (specific age unknown) adjoining the 10 year-old habitat showed this species to be present at Lebanon.

4--Acomys subspinosus was generally poorly represented, and was absent from 2 and 14 year-old habitats.

5--Insectivores were absent from 2 year-old fynbos; small numbers of Crocidura cyanea and C. flavescens were present only in the 4 year-old habitat, but Myosorex varius showed an almost linear increase with increasing age of the vegetation ($r = 0.985$; $P < .01$).

6--Praomys verreauxi and Elephantulus edwardii were respectively restricted to riverine and rocky outcrop habitats. P. verreauxi is, however, not generally restricted to riverine habitats, occurring on scrubby hill-slopes or forest margins in the Knysna area (Davis 1974), and on well-vegetated slopes in the Southern Cape mountains (Bond and others 1980).

7--The riverine small mammal communities were dominated by Otomys spp. and R. pumilio, and rocky outcrops by Aethomys namaquensis.

Relative biomass (fig. 3) was bi-modally distributed in the fynbos habitats, with peaks at 4 and 38 years. The high incidence of Otomys spp.

Table 2--Numbers of small mammals trapped in various S.W. Cape fynbos habitats.

Species	Montane fynbos - age in years					Mesic refuges	Rocky outcrops	Totals
	2	4	10	14	38			
Rodents:								
Acomys subspinosus		12	3		2	7		26
Aethomys namaquensis	23	4	2			11	14	54
Dendromus melanotis	6					1		7
Dendromus mesomelas			8		3	3		14
Mus minutoides	9					4	1	14
Otomys spp.	1	62	22	15	15	32		147
Praomys verreauxi						6		6
Rhabdomys pumilio	18	36		3	15	38		110
Insectivores:								
Crocidura cyanea		1				3		4
Crocidura flavescens		1				3		4
Elephantulus edwardii							2	2
Myosorex varius		3	16	12	27	14		72
Totals	54	119	53	30	62	122	17	460

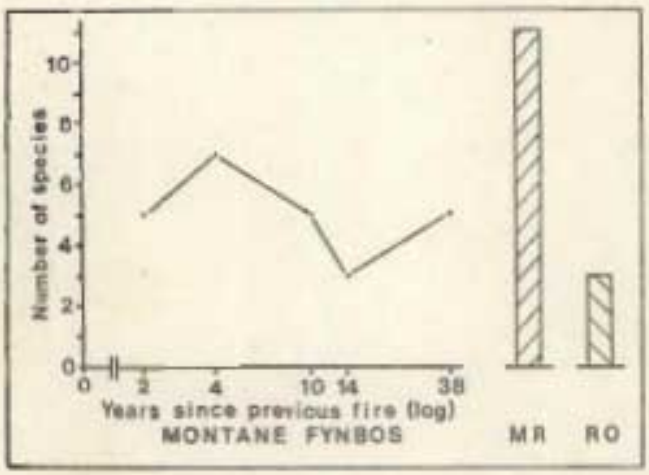

Figure 1--Species richness of small mammals in various S.W. Cape fynbos habitats. MR = mesic refuges; RO = rocky outcrops.

($\bar{X}$ = 99g) in 4-year-old fynbos (52 percent of total captures) and the reduced importance of this taxon at 28 years (24 percent), together with high 38-year numbers of M. varius (44 percent; $\bar{X}$ = 12g), largely explains the shift of the higher peak from 38 years (abundance; fig. 2) to 4 years (biomass; fig. 3). Relative biomass in the mesic habitats was identical to that in 4-year-old fynbos (19.0g/station-night), while rocky outcrops (2.5g/station-night) supported only 27 percent of the biomass of the next lowest habitat (10-year-old fynbos; 9.1g/station-night).

DISCUSSION

Successional Trends

The available data demonstrate the existence of bimodal distributions of small mammal species richness, abundance and biomass in respect of post fire age of montane fynbos, with early and late peaks, and intervening troughs. The de facto existence of a decline in middle-aged fynbos is supported by the fact that Taes (1972) recorded only 3 small mammal species in a 14 year-old Protea repens stand at Jonkershoek, and Lewis (in prep.) found only 1 species to be present at the same site when the vegetation was 17 years old. It is significant that small carnivores, as evidenced by tracks and scats observed during the present field work, and by interference with traps were only active in 4-and 38-year-old fynbos, and in riverine habitats, where small mammals were most abundant.

A similar bimodality has previously been described in humid montane grassland (Natal Drakensberg; Mentis and Rowe-Rowe 1979). These authors proposed that the reason for the bimodality they observed is that different species (including small mammals, antelope and francolin) are adapted either to frequently burned (fire accessible) or infrequently burned (fire inaccessible) habitats, but not to moribund habitats of intermediate post-fire age. It seems more economical to argue that some species are preadapted to recently burnt environments, exploit the resources available there and decline in the later seral stages. The second peak results from the presence of core species and those confined to old unburnt habitats.

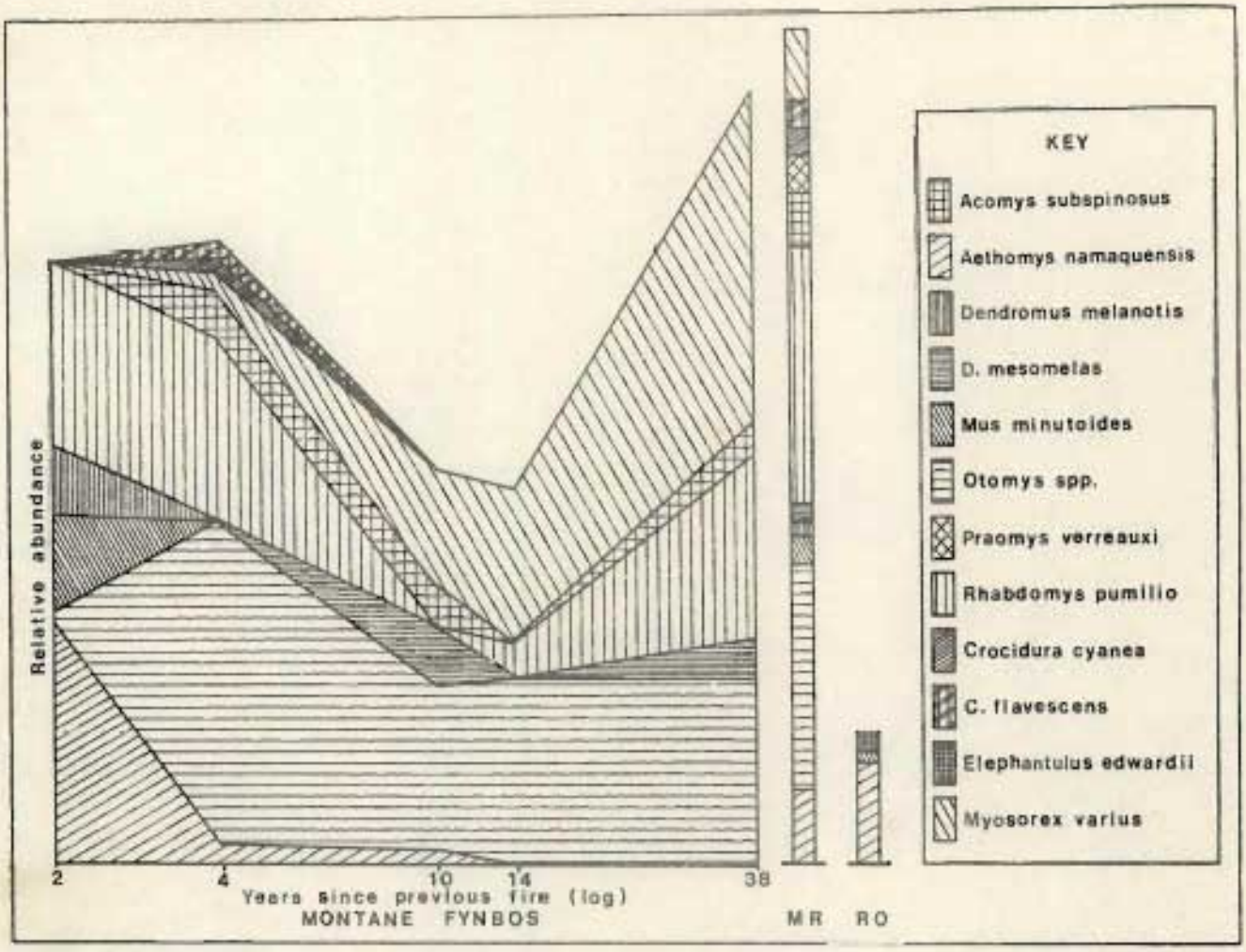

Figure 2--Relative abundance of small mammals in various S.W. Cape fynbos habitats. MR = mesic refuges; RO = rocky outcrops. Relative abundance calculated by dividing total captures for each species by sampling effort (station-nights).

On present knowledge the successional pattern in fynbos indicated by our results is not easy to explain fully. Limited cover and food may both restrict small mammal species richness and density on young burns. Cover requirements of Aethomys namaquensis are low and Rhabdomys pumilio prefers "grassy" ground cover, which includes Poaceae as well as the Cyperaceae and Restionaceae prominent in young fynbos (Bond and others 1980). The small size of Mus minutoides may enable it to use small residual patches of shelter (Bigalke and Willan in press). 4 of the 5 rodents trapped on the youngest burns (table 2) are omnivorous (Bigalke and Willan in press) and thus able to exploit whatever food resources are available. The fifth, Otomys sp., is a specialist herbivore and only becomes abundant later in response to increasing cover (see below).

Peak small mammal species richness, density and biomass measured at 4 years (table 2, fig. 2) is attained when the vegetation is reaching the end of its youth phase. During this time fynbos becomes dominated by restionaceous and graminoid plants and sprouting shrubs, the herbaceous plants reaching maximum biomass of up to 8000kg/ha. Canopy cover reaches about 80 percent of pre-burn levels and remaining sprouting species attain reproductive maturity (Kruger and Bigalke in press). Food resources are likely to be plentiful and of good quality. For some mammals abundant at this time cover density is known to be important. Bond and others (1980) found a positive correlation between the presence of Acomys and foliage density between 20 and 60cm although high elevation and rocky areas were also significant habitat factors in Baviaanskloof. Otomys spp. also exhibit a marked preference for dense shrubby vegetation (Bond and others 1980).

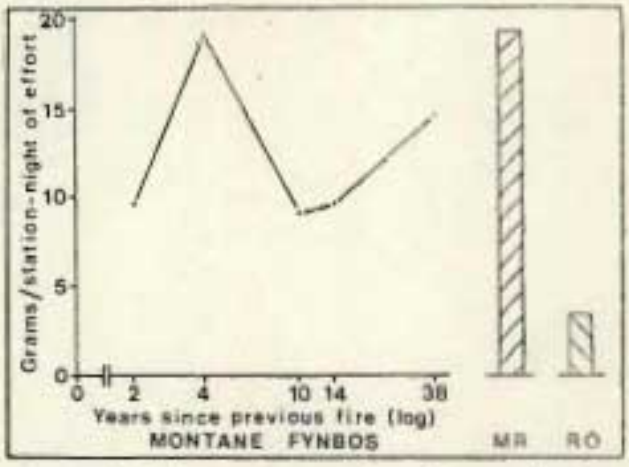

Figure 3--Relative biomass of small mammals in various S.W. Cape fynbos habitats. MR = mesic refuges; RO = rocky outcrops. Relative biomass calculated by dividing total biomass by sampling effort (station-nights).

The decline of small mammals in mature fynbos may reflect responses to dense canopy cover, the reduced importance of lower herbaceous strata and decreasing plant species diversity described by Kruger and Bigalke (in press). During the senescent phase of post-fire succession in fynbos - over about 30 years - these authors show that mortality among shrubs is high, the canopy opens and some seed regeneration may occur. A species such as Rhabdomys presumably again finds adequate food and "grassy" ground cover while the accumulated litter may be an important factor favouring Myosorex.

Recolonisation Rates

Rates of small mammal recolonisation of burns in fynbos appear slower than in other southern African ecotypes. The present study did not include habitats of less than 2 years post-fire age, but trapping on a burn at Duthie Reserve, University of Stellenbosch (33°56'S; 18°52'E; ± 100m), Bigalke and Pepler (unpubl.) found no small mammals to be present until Rhabdomys pumilio moved in 11 months after the fire. Taes (1972) sampled 1-year-old vegetation at Jonkershoek and found only 2 species to be present. In contrast, a number of studies in other regions have shown post-fire pioneer species to be present immediately after burning (Christian 1977; Kern 1978; Meester and others 1979; Mentis and Rowe-Rowe 1979), and as many as 5 species may be present 7 months after fire in Terminalio-Dichrostachys savanna (Kern 1978). These observations presumably reflect the slower rate of regeneration of fynbos relative to other vegetation types. It is of interest in this respect that of the species sampled in this study, 2 may be present immediately after fire in other ecotypes (Mus minutoides and Myosorex varius at Midmar Dam Nature Reserve, Natal - Meester and others 1979; Myosorex varius in the Natal Drakensberg - Mentis and Rowe-Rowe 1979). Other species in which post-fire pioneer status has been documented (Desmodillus auricularis, Gerbillurus paeba, Malacothrix typica - Christian 1977; Tatera leucogaster - Kern 1978; Praomys natalensis - Meester and others 1979, Mentis and Rowe-Rowe 1979) do not occur in the S.W. Cape. Further study may show that Aethomys nanoquensis, which as noted above is adapted to low cover densities (Bond and others 1980), survives on fresh burns. Its dominant position 2 years after fire (fig. 2) at least suggests that it recolonizes burns soon after fire. This species did not occur in the vicinity of Duthie Reserve, which represents a small fynbos "island" surrounded by disturbed and largely exotic vegetation.

Refuge Habitats

The data presented above indicate that riverine habitats are more important as refuges during and immediately following fire than are rocky outcrops. The occurrence in riverine vegetation of all 10 species found in the fynbos habitats suggests that recolonisation of burns at the appropriate stage of vegetative regeneration may occur from such refuges rather than surrounding areas of unburned fynbos, where species diversity may be low. In contrast, extensive recolonisation of fynbos from rocky outcrops would be expected to be undertaken only by Aethomys nanoquensis.

Conservation

The conservation status of the majority of southern African small mammals is unknown, but 4 species dealt with here (Acomys subspinosus, Otomys laminatus, O. saundersae, Praomys verreauxi) are rare (Dean 1978) S.W. Cape endemics (Davis 1974). Acomys and Praomys are pollinators of geoflorous proteas such as Protea amplexicaulis and P. humiflora (Niens and Rourke 1978). It seems reasonable to propose, therefore, that the local status of these species (at least) should be ascertained prior to prescribed burning, with a view to their conservation.

It has been shown that the abundance of francolin in the Natal Drakensberg is increased by burning small rather than large areas of veld, thus creating a fine mosaic of vegetation of different post-fire ages (Mentis and Bigalke 1979). Such a policy would appear to have much to recommend it, especially if consideration were given to the question of fire accessibility (Mentis and Rowe-Rowe 1979), so that naturally fire-accessible areas were burnt prior to reaching the moribund phase of vegetative succession, and succession was allowed to proceed ad infinitum in naturally fire-inaccessible areas. In the long term this would be expected to increase overall diversity, abundance, and biomass of small mammals, and hence to encourage proliferation of small carnivores and other predators which feed on them.

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Appendix 2

CHAPTER 14 *

EFFECTS OF FIRE REGIME ON FAUNAL COMPOSITION AND DYNAMICS **

R C Bigalke and K Willan

INTRODUCTION

In this paper an attempt is made to review the influence of fire - considering type and behaviour, season and frequency - on the composition and dynamics of fauna in Southern Africa.

Immediate direct effects are discussed first : To what extent does fire regime cause faunal change by mortality, dispersal or both? Indirect effects are then considered, distinguishing between those that are rapid and short-lived and those effective in the long term. What changes in species composition, species richness and population density arise from destruction of food resources or from increased availability or quality of food after a fire? What are the effects of alterations to vegetation structure and thus to the nature and amount of cover? How do changes in food and cover affect population structure and social organization?

Finally, evidence for postfire faunal succession is discussed in relation to plant succession and fire-induced changes in community structure and functioning and some aspects requiring further research are identified.

IMMEDIATE DIRECT EFFECTS OF FIRE

Fire can lead to faunal changes by killing animals or by causing them to disperse.

Mortality

Since even the most modest temperatures recorded in veld fires (eg Trollope 1981) are well above lethal levels for most living organisms, we might expect death from heat, or asphyxiation, to be quite common. Records of fire-induced mortality are nonetheless rare.

Responses of soil fauna have been little studied. By analogy with work elsewhere (Ahlgren 1974) it is likely that much of the soil mesofauna - mites, collembolans and other very small arthropods - as well as spiders, will be killed. However Lamotte (1975) states that fire does not greatly affect the fauna of the soil surface in tropical African savannas. Termites foraging in wood, but not those in the soil, are thought to have been killed in a broad-leaved savanna fire at Nylsvlei (Gandar 1979).

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** Manuscript not yet in final form - subject to further editing.

Some arboreal insects of the orders Hemiptera, Coleoptera and Lepidoptera survived in canopies of Dombeya rotundifolia trees 3 to 4m high but all were totally destroyed on Ochra pulchra trees of about 2m in height (Gandar 1979). The same fire resulted in a 30% decrease in grasshopper (Orthoptera Acrididae) biomass, although how much was due to mortality and how much to flight was not established. Y Gillon (1971) sampled grasshoppers immediately after a fire in tropical savanna on the Ivory Coast and recorded minimum figures of only 4,5% burned, 7,7% alive and 87,8% which had fled.

Y Gillon (1971) also reports that a spectacular variety of birds congregated about the fire, feeding on insects as they flew away from the flames. The effects could not be quantified. Insectivorous birds commonly gather at fires (eg Komarek 1969; Gandar 1979) and predation may be a significant additional cause of insect mortality.

Mortality may be high in flightless arthropods. Populations of the tick Ixodes rubricundus are reported to be significantly reduced by fire in mountains of the Karoo (Roux and Smart 1981), but this response is apparently not universal. Bosman (pers. comm) has shown that ticks in the Umfolozi Game Reserve in Natal have well adapted escape mechanisms, dropping to the ground in response to the presence of smoke. Among adult ticks at least, mortality seems to be low. Among grasshopper nymphs death rates ranging from 4,5% in an African savanna (Y Gillon 1971) to 100% in rangeland in the U S A (Hunter 1905) have been reported.

There are few records of fire-induced mortality among vertebrates. During a grassland fire at Midmar Dam Nature Reserve "a few" small mammals were killed or injured (C N V Lloyd, personal communication to K Willan). Wild fires in savanna in the Kruger National Park have killed or maimed about 40 mammals on each of two occasions. Species involved were elephant (Loxodonta africana), lion (Panthera leo), impala (Aepyceros melampus), kudu (Tragelaphus strepsiceros), waterbuck (Kobus ellipsiprymnus), steenbok (Raphicerus campetris), roan antelope (Hippotragus equinus), duiker (Sylvicarpa grimmia), and warthog (Phacochoerus aethiopicus) (Brynard 1971).

Dispersal

Dispersal of animals fleeing fire may be an important cause of faunal change. In tropical African savannas fire tends to lead to the disappearance of strongly flying insect groups, indicating either dispersal or mortality (Lamotte 1975). More specifically, the species composition of pentatomids (Hemiptera) in an Ivory Coast study area was altered through dispersal of strongly flying heliophilous forms and death of sciaphilous species, which fly only weakly.

Emigration was considered to be mainly responsible for a decline of 55 to 90% in small mammal density following a fire in Terminalia-Dichrostachys savanna (Kern 1978). Most impala left the burnt area and moved to other parts of the reserve in broadleaved savanna at Nylsvlei (Gandar 1979).

Effect of type and intensity of fire

The savanna fire in broadleaved savanna at Nylsvlei reported on by Gandar (1979) was of low intensity. Temperatures were significantly less than 250°C in the canopies of trees. This may explain why arboreal insects were totally destroyed on O. pulchra trees while some survived on taller individuals of D. rotundifolia. Direct effects on termites and beetle larvae in the soil were negligible. The fire which was applied at Nylsvlei burnt with an uneven front and left unburnt patches amounting to 21% of the area in which grasshoppers were studied. Mobile insects could escape through breaks in the fire front and shelter in unburnt patches. Grasshopper density in these patches was over 3 times prefire levels.

In contrast, conflagrations in the Kruger National Park, mentioned above, which caused the death of a variety of large mammals, followed 8 years of protection against fire (Brynard 1971). Dangerously high fuel loads of old grass had accumulated and about 25% of the Park's area was burnt out. Trollope (1981) believes the fires to have been fast moving, intense surface head fires with considerable flame heights through which even agile animals would have had difficulty escaping.

Effect of Season

Effect of burns at different seasons could vary considerably. For example, coming at a time when seasonally restricted activities were in progress, such as territory establishment, mating or breeding, fire would have a greater effect on populations than fires occurring at another time. There is little published information on this aspect. Gandar (1979) notes that the Nylsvlei fire took place in September when most grasshoppers were adult and so able to dodge the flames effectively. The implication is that mortality would have been greater had there been more immatures about. A fire mosaic of burns applied at different times of year maintains a richer and more varied insect population in tropical savanna on the Ivory Coast than areas burnt in only one season (D Gillon 1971).

Effect of Frequency

Type and intensity of fire are related to frequency and to the rate at which fuel accumulates which in turn depends on vegetation type and climate. There is little information available on the influence of different fire frequencies on direct fire effects.

One consideration leading to the introduction of more frequent burning in the Kruger National Park was the desire to reduce fire intensity to avoid conflagrations capable of killing large mammals (Brynard 1971). In the Hluhluwe-Umfolozi complex, much of which is burnt regularly on a cycle of 1 or 2 years, no ungulates were reported killed by fire from 1975 to 1977 (Brooks and Berry 1980). We have already noted the importance of refuges left by a patchy low intensity fire for grasshopper survival at Nylsvlei and of a fire mosaic of burns applied at different times of the year on insect populations in tropical savanna on the Ivory Coast (D Gillon 1971).

INDIRECT EFFECTS OF FIRE

Fire alters the physical environment and the nature and quantity of food and cover available to animals, while levels of competition and predation may also change. These factors greatly affect faunal composition and dynamics in the short term, much more so than the direct effects of a burn. The immediate consequences of a fire wane as postfire succession proceeds and the environment returns to its condition before the burn. The time scale of short-term changes is influenced by the rate of plant sucession and mean fire frequency, which may vary from less than a year in grassland to as long as 40 years in fynbos and longer in forest. Where fire modifies or drastically alters vegetation structure and composition, long-term faunal changes may occur.

Effects of short-term changes in Food Resources

Reduction of food supply. Fire may reduce or eliminate food supplies. For a month after the Nylsvlei fire foraging activity of termites was lower than usual, perhaps partly due to high surface temperatures on exposed soil and to dessication of the soil, and partly due to food scarcity (Gandar 1979). (Gandar 1979) also suggests a reduction in the supply of roots on which the larvae feed or of the quantity of carbohydrates contained in the roots (because of their diversion to newly stimulated top-growth), as factors accounting for a decline in the number of adult beetles emerging from the soil two months after a fire. Egg pods of grasshoppers and stick insects (Phasmidae) in the soil survived the fire but young nymphs emerging on burnt areas a month later generally did not survive.

The food preferences of the majority of South African small mammals in which responses to fire have been studied are poorly understood, but there is sufficient information to allocate them to one of three broad categories, omnivorous, herbivorous or insectivorous (Table 1). Comprehensive feeding studies have been undertaken only on Otomys irroratus and Rhabdomys pumilio (Curtis and Perrin 1979; Perrin 1980). In addition, digestive tract morphology and hence adaptation to diet, of a number of species listed in Table 1 has been investigated, and the feeding categories to which they were allocated (Perrin and Curtis 1980) are included in this table.

Fire may totally eliminate the food supply of the specialist herbivore O. irroratus and other Otomys spp. (Table 1), and their disappearance from burns may relate to food shortage. However, cover availability appears more important in the timing of recolonization (see below).

The remaining 17 rodent species under consideration here are omnivores but 6 of these are pioneer species in at least some areas, remaining on burns, while 11 are eliminated (Table 1). Similarly, while 3 of the 4 insectivores disappear, Myosorex varius may be present immediately after fire (Table 1). There are no published accounts of the specific dietary requirements of the majority of these species (ie except R. pumilio - Curtis and Perrin 1979; Perrin 1980), but of the 6 pioneer rodents (Table 1), 4 were dealt with by Perrin and Curtis (1980), who considered 3 to be true omnivores (eating seeds, green plant and invertebrate food) while the fourth was a granivore/ insectivore (eating mainly seeds and insects). Pioneer omnivores may change from primarily granivorous diets to herbivory, in accordance with prevailing

supply (eg Tatera leucogaster - Kern 1978). This species apparently crops the flush of green shoots appearing after fire. In spite of this, increased movement on burns relative to unburnt controls (Christian 1977a; Kern 1978) suggests that food supply is probably reduced by fire. Praomys natalensis, a primarily granivorous omnivore (Kingdon 1974) which pioneers a variety of disturbed habitats (de Wit 1972; Meester et al 1979), may immigrate onto burns (Hanney 1965; Neal 1970). This species was unable to maintain weight on laboratory diets comprising only green plant (kikuyu grass, Pennisetum clandestinum) or only invertebrate (Tenebrio larvae or Macrotermes nymphs) food (Willan in preparation). Rhabdomys pumilio lost weight on kikuyu grass, but gained weight on invertebrate food (Willan in preparation).

From the above it appears that species with the broadest food niches, at least among rodents, appear most likely to remain on burns immediately following fire (Table 1). However, elimination of a number of omnivores, albeit in at least some cases with narrower food niches than the true omnivore category (Perrin and Curtis 1980; Table 1), suggests that cover availability or some other factor or factors may be limiting in some cases.

Large herbivores move off burns, for example impala at Nylsvlei (Gandar 1979), as do common reedbuck in the Kruger National Park (Jungius 1971), but recolonization may be rapid (see below).

Increase in quantity and quality of food. For herbivores, regenerating vegetation soon provides a readily available source of palatable nutritious food and burns are often rapidly recolonized. Within a week two species of grasshopper appeared on the burn at Nylsvlei, one of them a mixed feeder which took not only grass, forbs and litter but also ash. Three more species were found after three weeks (Gandar 1979).

Rodent species trapped more frequently after a burn than before at Nylsvlei included Tatera leucogaster (but the percentage in the total catch did not change) and Saccostomus campestris. They were thought to be feeding mainly on surviving tree seeds (Gandar 1979). However, T. leucogaster takes green shoots as well; together with Steatomys pratensis it was found to immigrate onto triennially burnt plots in the months following a fire in the Kruger National Park (Kern 1978).

In burnt fynbos especially nutritious food resources, such as seed released from plants, corms, cormlets and other structures among geophytes, and sprouts are used by a wide variety of transients including birds such as Francolinus, Serinus and Streptopelia (Kruger, unpublished). Levyns (1929), and Kruger and Bigalke (1981), found increased rodent mole activity on burnt plots, presumably in response to greater availability of underground storage organs of geophytes.

New green growth appearing after fire attracts a wide variety of herbivores, from tortoises to lagomorphs and large ungulates, in all major vegetation types. Levyns (1929) observed "buck, a hare and several tortoises" foraging on recently burnt fynbos plots. Mountain reedbuck (Redunca fulvorufala), grey rhebuck (Pelea capreolus), and oribi (Ourebia ourebi), select strongly for the green flush of grass shortly following a fire in the Natal Drakensberg (Oliver et al 1978). Mentis (1978) showed that the crude protein and phosphorus content of this young regrowth is higher than in unburnt grass.

He also noted an apparent increase in population densities of grey rhebuck and oribi on a fine-scale mosaic of spring burnt and unburnt grassland with a network of firebreaks prepared annually in winter.

In savanna of the Hluhluwe-Umfolozi complex eight species of grazing ungulates were significantly attracted to winter and spring burns. Species responses were affected by their home range behaviour. Zebra (Equus burchelli), and buffalo (Syncerus caffer) with the largest home ranges, and wildebeest (Connochaetes taurinus) and square-lipped rhino (Ceratotherium simum) in which home ranges are medium-sized, moved rapidly onto burns. Waterbuck and warthog, which have small home ranges and which are closely associated with riverine habitats in winter did not move onto burns quickly (Brooks and Berry 1980). In this case, as with impala at Nylsvlei (Gandar 1979), a decline in the availability of young highly nutritive plant parts as the grass grew caused animals to move off. Peak impala numbers were observed 21 to 30 days after the fire at Nylsvlei. Thereafter numbers started decreasing gradually although density was still relatively high after 90 days. Brooks and Berry (1980) found differences between species in the stage of grass growth at which they abandoned the burns, related to their requirements for highly nutritive forage.

Feeding behaviour of springbok (Antidorcas marsupialis) and blesbok (Damaliscus dorcas) on burns reflects their requirements for increased food quality (Novellie 1978). On unburnt grassland mean feeding station interval (time spent at feeding station) was high on coarse mature swards high in crude fibre and low in crude protein levels. Feeding station intervals declined with seasonal reduction in fibre and increase in protein. On burns feeding station intervals were always low. The reasons proposed for this were the high nutritional value of resprouting grass, absence of obscuring mature plant parts and lower overall abundance of forage.

Predators may also benefit from conditions following a burn. At Nylsvlei Gandar (1979) found a concentration of grey hornbills (Tockus nasutus), which feed on grasshoppers, around the burn for a few weeks after the fire. The birds were exploiting insects exposed after the fire.

Effects of short-term changes in Vegetative Cover

Food supplies alone are not the only variable influencing animal populations after a fire. Changes in the amount and nature of vegetative cover may be at least as important, if not more so, although it is sometimes difficult to determine the relative importance of these two factors.

Reduction of plant cover and exposure of the soil surface may affect microclimate : thus high surface temperatures on exposed soils may have curtailed the time of day during which termites could forage near the surface on the Nylsvlei burn (Gandar 1979).

Increased insolation following removal of vegetation was partly responsible for drying of the soil, which may have been a factor in reducing emergence of adult beetles two months after a fire at Nylsvlei (Gandar 1979).

Lack of cover, together with food shortage and increased vulnerability to predation, are likely to be largely responsible for postburn declines or disappearances of small mammals (Delany 1972). Cook (1959) and Neal (1970) found these changes in small mammal populations to be related mainly to the effect of fire on cover. It follows that species which survive on burns (or rapidly recolonize them) are able to tolerate reduced cover levels. Four of the species listed in Table 1 as postfire pioneers include habitats with little cover in their normal ranges. Gerbillurus paeba, Desmodillus auricularis and Malacothrix typica are found, among other places, in sparsely vegetated areas of the Namib desert (Coetzee 1969), and Tatera leucogaster in areas of less than 70% cover or litter in Terminalia-Dichrostachys savanna in the Kruger National Park (Kern 1978). Similarly while P. natalensis occurs at a variety of cover densities (de Wit 1972; Willan in preparation), in some situations it may forage in the open (Kingdon 1974; personal observation by K Willan) in areas such as bare ploughed fields (Mendelsohn, unpublished). Hence, these four species appear pre-adapted to survive on burns. Mus minutoides and Myosorex varius are possibly sufficiently small (respectively approximately 8g and 12g) to avoid predators by making use of cover and refuges which are inadequate for larger species.

While the above provides possible reasons for the continued presence of pioneer species on burns, it fails to explain the elimination of the majority of specialist species (Table 1). There is some evidence, however, that specialists may be eliminated by insufficient cover rather than by shortage of other resources (Kern 1978). The specialist herbivores (Otomys spp.) have no food available to them immediately following fire, but the fact that they do not reappear for at least several months, during which considerable vegetative regeneration has usually occurred (eg Meester et al 1979; Mentis and Rowe-Rowe 1979), strongly implies a cover restriction in this case. Bond et al (1980) found a correlation between numbers of Otomys spp. and the presence of dense, shrubby vegetation. While not entirely restricted to high cover situations, O. irroratus appears to favour dense vegetation (Shortridge 1934; Roberts 1951; Davis 1973; Willan in preparation). Rhabdomys pumilio appears less cover-restricted than O. irroratus (Willan in preparation, but even in the desert grassland habitat studied by Christian (1977a), where R. pumilio would be expected to have evolved greater tolerance to low cover availability than in higher rainfall areas (D P Christian, personal communication to K Willan), it had not reappeared on a burn with 12 weeks.

Rhabdomys pumilio and O. irroratus, together with the majority of Otomys spp are unique among the species listed in Table 1 in that they normally nest on the surface, often under grass tussocks (Davis 1973; Brooks 1974) or other suitably dense vegetation; hence, removal of cover by fire would prevent norma nesting, and in itself would be sufficient to promote emigration from burns. In addition, R. pumilio, Lemniscomys griselda, O. irroratus and Otomys spp. are at least partially diurnal, with R. pumilio almost entirely so (Brooks 197 Christian 1977b). L. griselda (Kingdon 1974) and O. irroratus (Davis 1973) ar predominantly crepuscular. Thus, all three species are exposed to diurnal rap tors, which hunt by sight and are presumably more efficient at low than at hig cover densities. However, in compensation for increased predation by diurnal raptors, it is possible that predation by owls on crepuscular and noctural small mammals is reduced. Christian (1977a) noted the absence of Tyto alba an Bubo africanus from a burn but found that they hunted on a nearly unburnt control.

In the Natal Drakensberg, greywing (Francolinus africanus) and redwing (F. levaillantii) francolins are very rare or absent in cleanly burnt grassland (Mentis 1973; Mentis and Bigalke 1979), presumably in response mainly to cover destruction. Among fynbos birds the sugar birds (Promerops cafer), for example, depends on well-developed stands of Proteaceae about 8 years old and older for food and nest-sites. Fire deprives it of a habitable environment (Burger et al 1976; Mostert et al 1980).

As an example of a large mammal responding to cover changes, the case of common reedbuck (Redunca arundinum) in the Kruger National Park may be quoted. Jungius (1971) found reedbuck to vacate areas in which the tall grassland they inhabited was totally destroyed by fire. Old territories were abandoned and males competed for new sites in localities where food and cover was still available, such as gallery bush along river courses or remnant grass patches. Social reorganization included the formation of new associations between territorial males, females and juveniles.

Long-term Changes

Fire may drastically alter vegetation structure and so create long lasting or even permanent faunal changes. Perhaps the most dramatic example is the destruction of forest with its dependent fauna. The extent to which forest cover has been eliminated is discussed by Granger (1981). Fire-maintained climax grassland supports a grassland fauna.

In savanna and woodland, fire can alter the density of woody species and the grass-bush balance. For example Trapnell (1959) reports that 23 years of early burning in June and July maintained closed canopy Brachystegia-Julbernandia woodland. Late burning in October thinned out the woody vegetation and led to increased grass cover. Bush encroachment, which resulted from frequent early dry season burning (and grazing) in the Kruger National Park, was accompanied by a decline in grazing ungulate populations and an increase in browsers (Brynard 1964).

Influence of fire regime on indirect effects

Type and intensity of fire. While one might expect the most intense fires to create the least favourable postburn environments for animals, evidence supporting this is limited. The low-intensity patchy burn at Nylsvlei merely scorched leaf litter. Beneath it Odontotermes and Thysanura were found foraging shortly after the fire. The litter also served to protect tree seeds on which Saccostomus campestris and Tatera leucogaster were able to feed. Unburnt patches of grass provided food and cover for grasshoppers (Gandar 1979). In contrast, a fire as intense as that in the Cedarberg in January 1975, which killed most resprouting herbs (Kruger and Bigalke 1981), might be expected to have destroyed most animal food and cover.

Season of burn has a particularly striking effect on food in sour grassveld, where nutritive values are at their lowest in the coldest, driest months. From August to October, mortality amongst small antelopes reaches a peak in montane grassland of the Natal Drakensberg (Mentis 1978; Oliver et al 1978). There is evidence that the higher crude protein and phosphorous content of this grassland burnt in autumn reduces antelope mortality and that a change from predominantly autumn to spring burning has led to a decline of antelope numbers in Giant's Castle Game Reserve (Scotcher et al 1979).

Eight species of grazing ungulates were equally attracted to winter and spring burns in the Hluhluwe-Umfolozi complex. Mixed feeders (nyala and impala) showed a preference for spring burns. This may be because both species switch from browse to graze at the beginning of the rains and thus become less dependent on riverine habitats (which were not burnt) at that time (Brooks and Berry 1980).

Frequency. Fire frequency influences the quality of pasture for herbivores to varying degrees in different vegetation types and climatic zones. For example, when a policy of burning not more than once every 5 years was introduced in the Kruger National Park, it led to the accumulation of moribund grass and emigration of grazing ungulates. Subsequently burning frequencies ranging from annual or biennial in moist sourveld areas to once every 4 to 8 years in dry sweetveld were instituted to maintain acceptably short palatable grazing (Brynard 1971; Gertenbach 1979).

Food and cover are probably both involved in the response of mammal and bird populations to fire frequency in Drakensberg montane grassland. Mentis and Rowe-Rowe (1979) found the greatest abundance and species richness of francolin, small mammals and antelope up to 3 years after fire. Thereafter numbers of both species and individuals were low (but another peak was found in fire-protected areas). Protection of grassland from defoliation for 2 or more years renders it unattractive to guineafowl for nesting (Mentis 1972).

Fynbos fires frequent enough to prevent regeneration of fynbos to the shrubland stage, required for example by the sugar bird (see above), would effectively exclude this species.

In summary, fire frequency determines how often vegetation is returned to the beginning of the postfire successional process, when food supplies for various species are either diminished or improved and when low cover availability encourages some species and excludes others. Changes in community composition reflect this and are probably most strongly influenced by frequency.

FIRE EFFECTS ON POPULATION STRUCTURE AND SOCIAL ORGANIZATION

Immediately following fire, vulnerability of grasshopper nymphs to predation on exposed areas, together with food shortage, combined to increase mortality so that the grasshopper population after the Nylsvlei fire consisted mainly of large old individuals (Gandar 1979).

One might expect food shortages to reduce reproductive success in many species, and competition on burns or in refuges to increase juvenile mortality, but these speculations require confirmation.

Social organization may be disrupted in various ways. Home range sizes of Gerbillurus paeba and Desmodillus auricularis (Christian 1977a) and Tatera leucogaster (Kern 1978) increased after fire. Animals emigrating from burns must be expected to affect social organization in the unburnt habitats they invade. Thus many reedbuck abandoned their old territories and males competed for new sites in remaining refuges. The period of social reorganization saw the formation of new associations between territorial males, females and juveniles (Jungius 1971). Impala formed large aggregations on the Nylsvlei burn (Gandar 1979).

It may be significant that of the three South African small mammal species whose social systems have been studied, one, Praomys natalensis, is highly sociable and nonterritorial (Cilliers 1972; de Wit 1972) and may remain after fire. Otomys irroratus and Rhabdomys pumilio include territoriality in their complex social organizations (Davis 1973; Brooks 1974; Marais 1974) and are eliminated from burns. Sociability may perhaps rank with a broad feeding niche and tolerance of low cover as a preadaptation to burns.

POSTFIRE SUCCESSION

Mortality, dispersal and responses to changes in food, cover and predation result in altered postfire communities. Available information on the nature and tempo of successional changes is reviewed here.

Initial Phase

Early postfire communities studied to date are characterized by reduced species richness, population density and biomass. In Namib desert grassland five rodent species were present on a control plot but only three on a burn (Christian 1979). Two small mammal species were trapped shortly after a fire in montane grassland, compared with seven 18 to 24 months later; postburn population density was low (Mentis and Rowe-Rowe 1979). Meester et al (1979) trapped only one rodent species three months after a fire in grassland near Cathedral Peak. In Terminalia-Dichrostachys savanna a single species of rodent was trapped two weeks after a fire and a second was present at two months. Peak small mammal biomass on annual burns was only about half that on unburnt controls (Kern 1978). Grasshopper biomass in a mosaic of burnt and unburnt patches of Burkea savanna immediately after a fire was 70% of that of unburnt savanna. It declined to 44% after six weeks and was 42% after four months (Gandar 1979). In transitional Coastal Renosterveld at Stellenbosch one species of small mammal was present in the first year after a burn, compared with four in the second and 6 to 7 in subsequent years. Trap success was 3,6% in 1 to 2 year old veld but 50,4% at age 3 - 4 years. (R C Bigalke and D Pepler, unpublished).

Primary consumer species present in the early stages after a fire tend to be unspecialized feeders tolerant of sparse vegetation cover. From the first week after the Nylsvlei fire two grasshopper species reinvaded, Acrotylus diana, a cryptically coloured species favouring open habitats, and Acorypha pallidicornis, a mixed feeder eating grass, forbs, litter and - on the burn - ash. There was evidence that these and other grasshoppers fed less selectively on burnt areas (Gandar 1979).

It has already been pointed out that rodents found on fresh burns tend to be those with broad food niches. Most also include habitats with little cover within their normal ranges, for example Gerbilturus paeba, Desmodillus auricularis, Malacothrix typica, Tatera leucogaster and Praomys natalensis. Small mammal ploneers which do not fall into this category - Mus minutoides and Myosorex varius - may be sufficiently small to avoid predation by making use of cover or refuges inadequate for larger species.

That predation is important is suggested by the fact that most small mammals using fresh burns are nocturnal or crepuscular. Furthermore, diurnal grasshoppers were exposed to opportunistic predation by hornbills congregating at the Nylsvlei burn (Gandar 1979).

Temporary Aggregations

In apparent contradiction of the trend towards species-poor, low density communities following a fire, species exploiting abundant ephemeral resources may become common for a while. About three weeks after the Nylsvlei fire the grasshopper fauna was augmented by the appearance of three more species. Another two followed a few weeks later (Gandar 1979).

Large herbivores often aggregate in spectacular fashion. At Nylsvlei impala began to appear in increasing numbers 11 to 20 days after the fire and reached a peak at 21 to 30 days. They shifted their preference from Acacia communities which were not burnt - to normally nutrient-poor Burkea which were usually avoided (Gandar 1979). Eleven species of ungulates were attracted to burns in the Hluhluwe-Umfolozi complex, eight of them to a marked degree (Brooks and Berry 1980). If limited areas are burnt high population densities may be attained and management must ensure that burns are large enough to avoid overgrazing (Edwards 1981).

Aggregations of large grazers are a temporary phase in postfire succession. Impala numbers at Nylsvlei decreased gradually from 30 days after the fire, although they were still relatively high after 90 days (Gandar 1979). In Zululand, species left when the burn no longer provided shorter, more palatable grazing than surrounding veld. The order of their going corresponded to their tolerance of long grass, warthog being the first to leave, zebra and buffalo the last (Brooks and Berry 1980).

Transients may also exploit seed released from plants, corms and sprouts, as do birds such as Francolinus, Serinus and Streptopelia in fynbos. In this vegetation rodent moles also increase in abundance presumably in response to increased abundance or availability of geophytes after fire (Kruger and Bigalke 1981; Levyns 1929). Predators too may congregate temporarily. As noted above, Gandar (1979) found grey hornbills to be unusually abundant for several weeks after the Nylsvlei fire, preying on grasshoppers which were readily available.

Succession over the longer term

Successional changes are best documented for small mammals. They accompany and are apparently mainly the result of postfire changes in vegetation structure. Fig. 1 summarizes data relating to species richness from seven different studies (Toes 1972; Christian 1977a; Kern 1978; Mentis and Rowe-Rowe 1979; Lewis in preparation; Willan and Bigalke in preparation; R C Bigalke and D Pepler unpublished). The data of Toes, Lewis and Willan and Bigalke are combined since they sampled similar habitats using similar techniques.

Three trends are indicated in Fig. 1.

1. Species richness increased with time (but see point 3 below).

2. Rates of change are variable. Initially fewest species are present in fynbos (data sets 4, 5) and most in desert grassland (data set 1), where the three trapped immediately after the fire are adapted to low-cover environments (see above). Change was most rapid in Terminalia-Dichrostachys savanna in the Kruger National Park where five species were present seven months after burning (data set 2) but species richness was greatest in montane fynbos at 2 to 6 years (data set 4).

3. In the two studies including relatively old postburn vegetation (humid montane grassland, data set 3; montane fynbos, data set 4) two peaks of species richness are evident. In grassland the second is attained earlier than in fynbos, a fact explicable by the slower rate of vegetation change in fynbos (Kruger and Bigalke 1981). Mentis and Rowe-Rowe (1979) have suggested that this bimodality is the result of small mammal and antelope species being adapted either to frequently burnt or fire inaccessible grassland habitats but not to those of intermediate age. A simpler explanation is that some are preadapted to exploit postburn environments and decline in the absence of fire; others are restricted to stable vegetation seldom disrupted by burning.

Changes in species composition are also related to plant succession. In Terminalia-Dichrostachys savanna burnt triennially, Tatera leucogaster was dominant while cover was less than 70% and there was little litter. By the end of the cycle, when very dense cover and litter had developed, the shrew Crocidura hirta was the dominant small mammal (Kern 1978). Similar patterns of change are reported from montane grassland (Mentis and Rowe-Rowe 1979) and fynbos (Willan and Bigalke in preparation). Re-emergence of a shrub canopy in fynbos provides habitat suitable for sugar birds (Mostert et al 1980) and presumably also for other birds. Cody (1975) found species richness to be directly related to structural diversity of fynbos vegetation.

Abundance of small mammals as indicated by trap success has also been found to exhibit a bimodal distribution in montane grassland (Mentis and Rowe-Rowe 1979) and montane fynbos (Willan & Bigalke in preparation), with the grassland peak occurring earlier than that in fynbos. In Kern's (1978) Kruger National Park study unburnt controls maintained a high stable density and biomass (and species composition) while in annually burnt plots the seasonal peak biomass was only half that of control plots.

In summary, available evidence suggests the following sequence of successional stages after a burn:

1. Survival of or rapid recolonization by a few species with broad feeding niches and which are tolerant of open habitats; densities and biomasses are low.

2. A more or less strongly developed phase of temporary aggregation by opportunistic species exploiting ephemeral food resources. High biomasses may be attained.

3. Gradual increase in species richness and population density as structural diversity of vegetation increases, with loss of some pioneers and appearance of species whose niche requirements are now met.

4. In the continued absence of fire, at least in montane grassland and fynbos, further species may be lost and density and biomass may decline, to increase again in the long term if and when an essentially different type of community has developed.

It is worthy of note that successional changes may be influenced by fire behaviour and especially by the patchiness of a burn, which is linked to frequency, and by season. The effect of area of burn may be significant but has not been studied.

CONCLUSIONS

Much less is known about faunal responses to fire than is known about the response of flora and vegetation. Available data come from a few widely scattered localities and relate mainly to some insects, birds and mammals, so that it is difficult to make satisfactory generalizations.

Fire appears not to kill many animals directly but more often results in significant dispersal. Type and intensity of a burn and the extent to which it leaves unburnt refuges are important variables affecting survival, especially of species of limited mobility. Scale is also likely to have a marked effect but has not been investigated. The inhospitable postburn environment has little cover and at first offers little food to primary consumers. Predators may however find abundant prey during and after a fire and may be an important contributory factor to the decline in animal density typical of fresh burns.

As the vegetation regenerates, temporary aggregations of primary consumers, especially large mobile forms, may exploit the accessible and palatable resources of high quality food which becomes available. At a time of year when unburnt vegetation is of particularly low nutritive value, as for example in the cold dry season in montane grassland, burns may significantly affect survival of antelope, and possibly of other species as well, by making green pasture available.

Change in vegetation structure, most marked in fynbos, appears to be the main feature influencing changes in species composition and population density in the course of postfire succession. From sparse populations of few species adapted to open habitats and using a wide spectrum of foods, communities grow in density and complexity. In high rainfall grassland and fynbos, where the phenomenon has been studied, species richness and population densities decline in the continued absence of fire, the time scale depending on rate of vegetation regeneration. Fire at appropriate frequencies thus maintains high species richness and density. Late seral species may however be eliminated by too frequent burning and a spectrum of habitats of different postburn ages is probably required to maintain maximum faunal diversity. The scale of such a mosaic is likely to be important, especially to species of limited mobility requiring a diversity of vegetation forms within home ranges. Critical studies of faunal responses to burns at different intervals and seasons and on varying scales are needed.

Little is known of the effects of fire regime on population dynamics. Enhanced reproductive success and survival may be expected initially for recolonizing species with access to high quality food and little competition. Dispersal may be significantly affected. Topics such as levels of inter- and intraspecific competition and predator-prey interactions on burns have not been studied. On many fronts there is a need for more research, particularly in order to provide a scientific basis for use of fire for faunal conservation and management.

Table 1

Postfire successional status and feeding categories of some South African small mammals. Succession : S = specialist; P = pioneer (for additional description see text). Diet : O = omnivore; H = herbivore; I = insectivore; O/H = omnivore with tendency to herbivory (14); G/I = granivore/insectivore, consuming large amounts of insects and seeds (14). Numbers 1 - 19 are references.

SPECIES	SUCCESSIONAL STATUS	DIET	DIGESTIVE TRACT MORPHOLOGY
RODENTS			
Acomys subspinosus	S (18)	O (1,7)	
Aethomys chrysophilus	S (9)	O (7)	O/H (14)
Aethomys namaquensis	S (16)	O (1)	O/H (14)
Dendromus melanotis	S (13, 16, 18)	O (7, 19)	
Dendromus mesomelas	S (16)	O (7, 19)	
Desmodillus auricularis	P (8)	O (11)	G/I (14)
Gerbillurus paeba	P (8)	O (11)	
Lemniscomys griselda	S (9)	O (1,7)	O/H (14)
Malacothrix typica	P (8)	O (1)	
Mus minutoides	P (12); S (13,18)	O (7, 10)	O (14)
Praomys natalensis	P (2,3,4,11,12) S (9)	O (7,17)	O (14)
Praomys verreauxi	S (16)	O (1)	
Otomys irroratus	S (12,13,16)	H (5,15,17)	H (14)
Otomys spp.	S (16,18)	H (1,16)	
Rhabdomys pumilio	S (8,12,13,16,18)	O (6,15,17)	O (14)
Saccostomus campestris	S (9)	O (1,7)	G/I (14)
Steatomys pratensis	S (9)	O (7)	G/I (14)
Tatera leucogaster	P (9)	O (7)	O (14)
Thallomys paedulcus	S (12)	O (7)	O (14)
INSECTIVORES			
Crocidura cyanea	S (16)	I (1)	
Crocidura flavescens	S (13,16,18)	I (1)	
Crocidura hirta	S (9)	I (1)	
Myosorex varius	P (12,13); S(16,18)	I (1)	

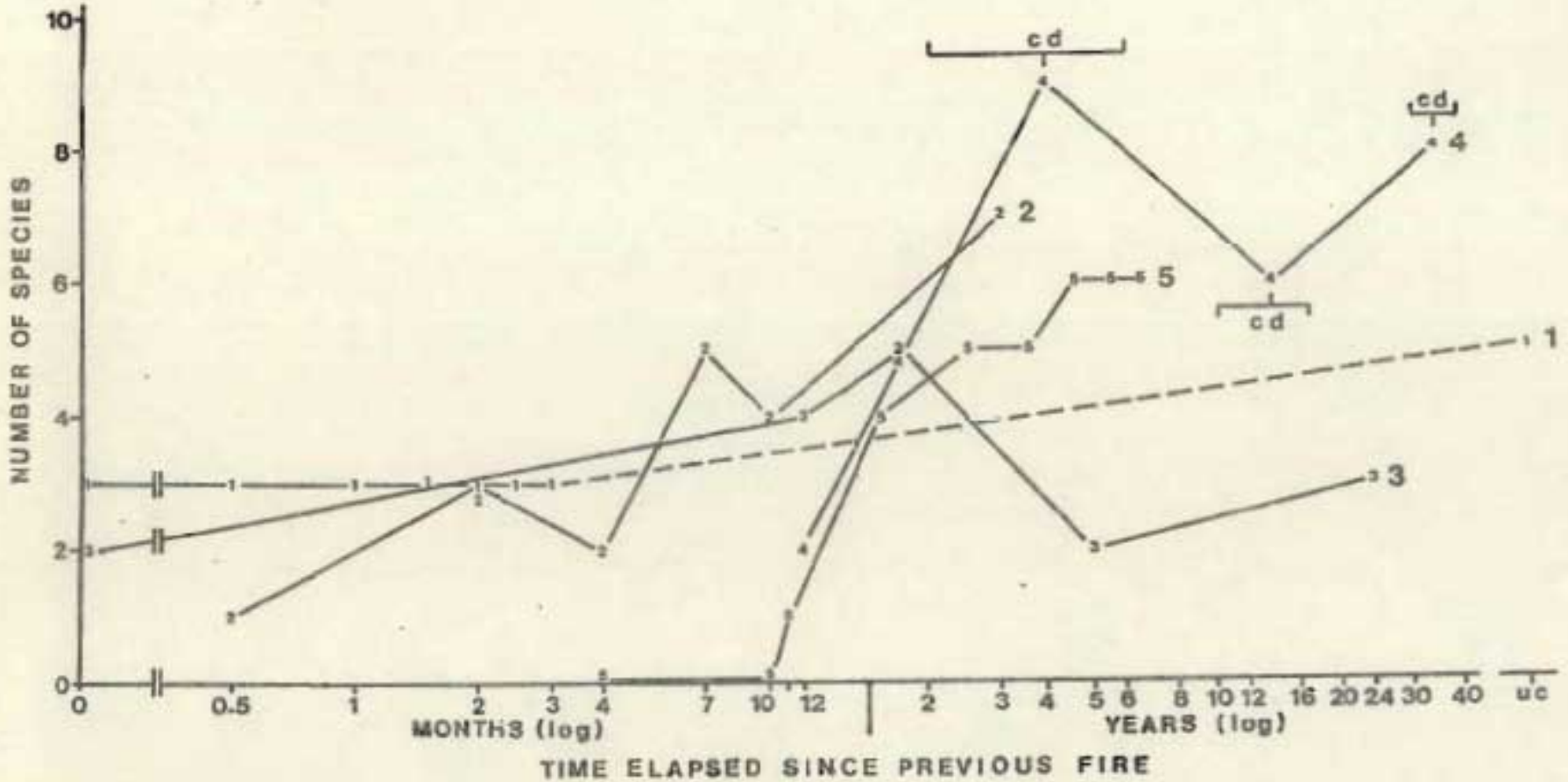
1. Roberts (1951)
2. Hanney (1965)
3. Neal (1970)
4. Delany (1972)
5. Davis (1973)
6. Brooks (1974)
7. Kingdon (1974)
8. Christian (1977a)
9. Kern (1978)
10. Willan and Meester (1978)
11. Christian (1979)
12. Meester et al (1979)
13. Mentis and Rowe-Rowe (1979)
14. Perrin and Curtis (1980)
15. Perrin (1980)
16. Willan and Bigalke (in preparation)
17. Willan (in preparation)
18. R C Bigalke D Pepler (unpublished)
19. K Willan (Personal observation)

CAPTIONS

Fig. 1

Number of small mammal species in relation to time elapsed since previous fire.

1. Desert grassland (Christian 1977a)
2. Terminalia-Dichrostachys savanna (Kern 1978)
3. Humid montane grassland (Mentis and Rowe-Rowe (1979)
4. S W Cape montane fynbos (Toes 1972; Lewis in preparation; Willan and Bigalke in preparation)
5. S W Cape fynbos "island" (R C Bigalke and D Pepler unpublished), uc : unburnt control of unspecified age, cd : combined data for the period indicated.


NUMBER OF SPECIES
10
8
6
4
2
0
cd
cd
cd
1
2
3
4
5
0
0.5
1
2
3
4
7
10
12
2
3
4
5
6
8
10
12
16
20
24
30
40
uc
MONTHS (log)
YEARS (log)
TIME ELAPSED SINCE PREVIOUS FIRE

A23

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Design and field tests of a modified small mammal livetrap

K. Willan

A PVC (poly-vinyl-chloride) and metal small mammal live-trap has been developed and subjected to field tests. The PVC traps captured greater numbers of very small rodents and shrews but fewer large rodents than did hardboard ones.
S. Afr. J. Zool. 14: 81-84 (1979)

'n PVC-en-metaal vanghok vir klein soogdiere is ontwikkel en is aan toetse in die veld onderwerp. Hierdie PVC-vanghokke is meer doeltreffend wat kleiner knaagdiere en spitsmuise betref; kartonplankvanghokke is egter meer geskik vir die groter knaagdiere.
S.-Afr. Tydskr. Dierk. 14: 81-84 (1979)

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The factors influencing trapability of small mammals, including the type of trap used, have been reviewed by Flowerdew (1976). Traps of similar design but different sizes may elicit differential response (Quast & Howard 1953; Wingate & Meester 1977) and even apparently identical traps may yield significantly different numbers of animals due to varying responsiveness of their tripping mechanisms (Grant 1970). Differences in trap efficiency for different species and castes (e.g. males, females, juveniles) necessitate proving in field trials that traps adequately perform the tasks for which they are used (Wiener & Smith 1972). In one of the few trap-response studies that have been done under African conditions Wingate & Meester (1977) established that of six types of livetrap tested, hardboard boxtraps 270 x 90 x 85 mm (Meester 1970) were most effective in capturing *Rhabdomys pumilio* and *Praomys natalensis*, while *Otomys irroratus* was most frequently captured in wire-mesh 'Tomahawk' traps 310 x 135 x 140 mm. Davis (1973) found hardboard traps to be most successful for *O. irroratus*. Although hardboard traps are commonly used in South African small mammal field studies (e.g. Davis 1973; Brooks 1974; Lloyd in prep.) they have a number of major disadvantages. Among these are their weight (approximately 700 g), lack of long-term durability, and the high labour costs involved in their construction. Accordingly a PVC (poly-vinyl-chloride) and metal tunnel trap was developed which appears in some ways to be an improvement on hardboard traps, or at least a useful addition to the range of livetraps available. A modification of the hardboard trap (Meester 1970), it is weatherproof, cheap and simple to construct, and in field trials described below proved to sample very small mammals more effectively than did hardboard traps.

Design and construction of PVC tunnel traps

The trap (Fig. 1) is based on the design of hardboard tunnel traps (Meester 1970). The 216 mm tunnel consists of 2 mm rectangular 54 x 68 mm PVC 'Classic' downpipe (Marley S.A. (Pty) Ltd), cut from 4 m lengths on a circular saw fitted with a perspex-cutting blade. Using a 4 mm tungsten-tipped blade, the tunnel was grooved across the 54 mm top and bottom 6 mm from one end to a depth of 5 mm to hold the sliding door at the back of the trap. Jigs were

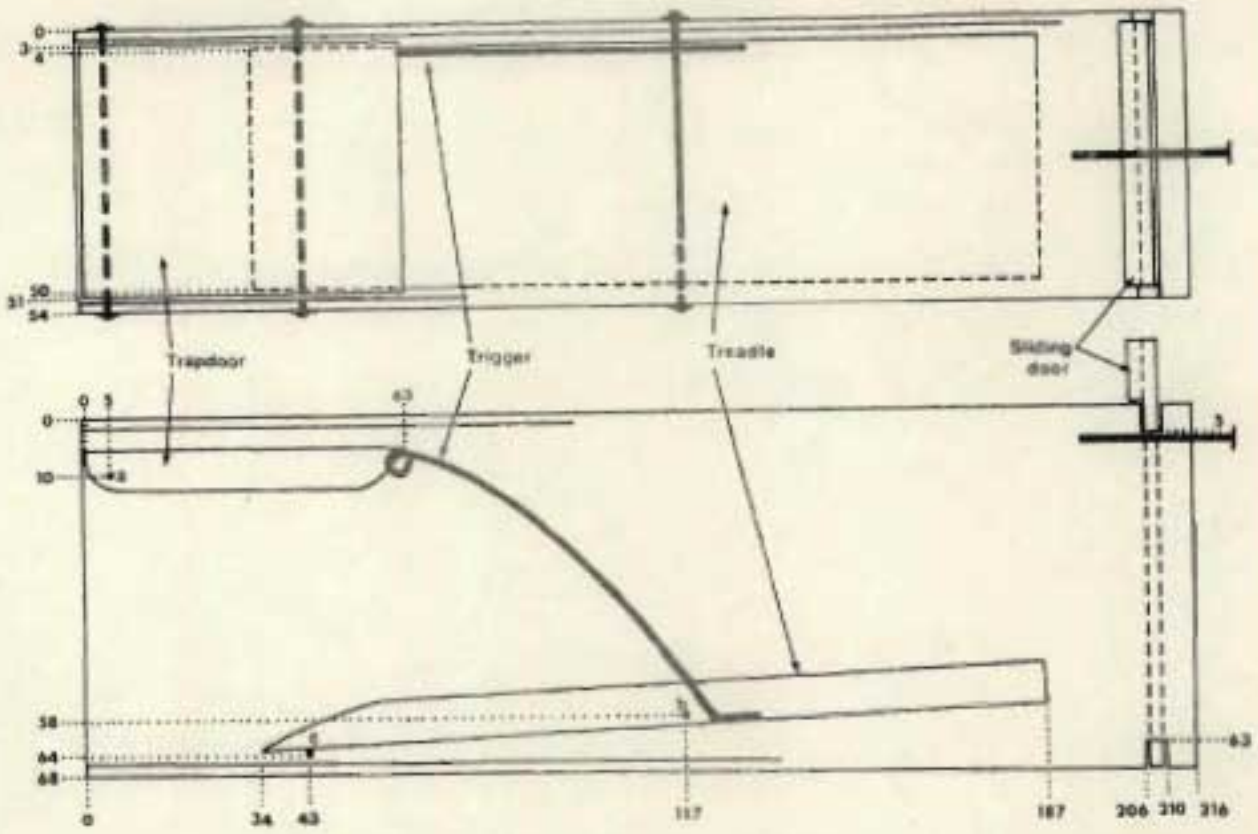

Fig. 1 Design of PVC and metal tunnel traps (after Meester 1970). Figures along both axes represent distances in mm. For construction details, see text.

constructed to facilitate drilling with a drill-press of three pairs of 1,5 mm holes according to the placement of points a, b and c (Fig. 1). The trapdoor was constructed of 0,9 mm aluminium and the treadle of 0,8 mm brass sheeting, and the appropriate holes (a and b) were drilled prior to bending. The trigger was made of 1,5 mm brazing rod soldered into position and bent into the appropriate shape.

The trapdoor and treadle were hinged by means of 56 mm pieces of 1,5 mm brazing rod fixed in position with a 1,5 mm brass washer soldered onto each end. The third cross-member (c, Fig. 1) was added to reduce the minimum distance between the front of the treadle and the bottom of the trapdoor to approximately 2 mm as the door pivotted. This was done in an attempt to ensure that captives attempting to lift the trapdoor to escape would be prevented from doing so by their paws jamming, thus thwarting attempts to open the door. The sliding door was made of 3 mm perspex 49 x 80 mm with a 12 mm perspex strip fixed to one end with 'Tensol 6 cement'. With the door in position, a 2 mm hole was drilled through the perspex immediately below the inner edge of the tunnel to allow locking of the door with a 32 mm nail. With the exception of the nail only non-ferrous metals were used to obviate the possibility of rusting. The final weight of the trap is approximately 250 g and construction cost, excluding labour, was approximately 60 cents per trap in 1976 when they were made.

Using traps as described above to collect shrews R.M. Baxter (pers. comm.) greatly reduced mortality by providing nesting material, food and water in plastic boxes 155 x 120 x 85 mm cut to fit into the grooves for the sliding door. These traps are probably too small for general purpose trapping, and the design may be adapted to use of PVC '4-square' downpipe 65 x 78 mm (Durapenta). Alternatively, it has been suggested by an anonymous referee of my manuscript that PVC mains conduit 72 x 65 mm, which has a sliding top, be used. This would obviate the need for a movable door at the back as the sliding top would give access to the moving parts and captured specimens. Making such traps 300 mm in length, with the moving parts well forward, would allow nesting material to be provided at the back of the trap.

Relative effectiveness of PVC and hardboard tunnel traps

Materials and Methods

In January 1977 a trapping study in largely undisturbed grassland at Dargle State Forest, Natal (29° 32' S, 30° 01' E; ± 1 500 m) provided the opportunity of testing the relative efficiency of PVC and hardboard tunnel traps. The following species were trapped: *Otomys irroratus*, *Rhabdomys pumilio*, *Mus minutoides*, *Crocidura flavescens* and *Myosorex varius*. Traps baited with rolled oats and raisins were set in pairs, one PVC and one hardboard, within 1 m of one another and within 1 m of station markers along two 20-station traplines and on a 10 x 6-station grid with 10 m between stations. Traps were checked morning and evening providing a total of 1 960 trap-checks. Trap preference and mass to the nearest 0,1 g were noted for all captures and animals were released at the point of capture.

Results

A total of 203 captures was made, 104 in PVC and 99 in

hardboard traps. This difference is not significant (x^2 = 0,12; ,80 >p>,70) but the difference in mean mass of animals captured in PVC (36,2 g) and hardboard (67,5 g) traps is very highly significant (t_{30} = 8,63; [illegible]>p). Numerical breakdown by species and into mass classes are given in Table 1, together with x^2 values, p and levels of significance. The mass classes were selected so that the first (animals under 15,0 g) contained all *Mus minutoides* and *Myosorex varius*, and the last (60,0 g and over) contained only *Otomys irroratus*. Animals under 15,0 g in mass were captured significantly more often in PVC traps while those of 60,0 g and over were most frequently captured in hardboard traps (Table 1). Captures assigned to the three classes between 15,0 g and 59,9 g numerically favoured PVC traps but the differences were not statistically significant. However, captures for the four classes 0 - 59,9 g combined statistically favoured PVC (87 animals) rather than hardboard (35 animals) traps (x^2 = 22,16; ,001>p). *O. irroratus* was most frequently captured in hardboard traps, and *Mus minutoides* and *Myosorex varius* in PVC traps. *Rhabdomys pumilio* and *Crocidura flavescens* had greater capture frequencies in PVC traps but there were no statistical differences in the case of these species.

Discussion

It is apparent that PVC tunnel traps 216 x 54 x 68 mm selectively captured the smaller animals occurring in the Dargle study area, while hardboard traps 270 x 90 x 85 mm were more effective for larger ones, specifically *Otomys irroratus*. This ambivalence is probably explained by the greater sensitivity of the trigger mechanism of the PVC traps. Wingate & Meester (1977) quote C.N.V. Lloyd (pers. comm.) as finding nesting material in hardboard traps together with *Myosorex varius* females, suggesting that they were able to enter and leave the traps a number of times before triggering occurred. Similarly Willan & Meester (1978) found it necessary to use tunnel traps 30 x 40 x 200 mm with extremely sensitive triggering mechanisms in order to consistently trap *Mus minutoides*. However, it is unlikely that trigger sensitivity is the only factor determining trap success, particularly in the case of larger animals, such as *O. irroratus*, which may be inhibited from entering traps of small size. Of the 85 *O. irroratus* captured during the study, 12 weighed over 150 g and it is significant that all of these were taken in hardboard traps (x^2 = 12,0; ,001>p). However, of 35 *O. irroratus* weighing under 100 g, 24 were captured in hardboard and 11 in PVC traps. Although this distribution tends more toward randomness than that for animals over 150 g or for the species as a whole (Table 1) the difference is significant (x^2 = 4,83; ,05>p>,02).

It may be concluded that although the PVC traps sampled *O. irroratus* less efficiently than did the larger hardboard ones, they were superior in respect of smaller species and may prove useful used in conjunction with larger traps in order to obtain unbiased field estimates (Sealander & James 1958). Alternatively, adaptation of the design presented here to PVC tunnels of larger dimensions should result in a more versatile, durable and efficient trap suited to efficiently sampling animals of a wider range of sizes.

Acknowledgements

Suggestions leading to design improvements were made by Professor J. Meester, Mr R.M. Baxter and Mr D.P. Campbell, and Mr Campbell assisted with construction of the traps. Ms J. Willan assisted with the field tests and typed the manuscript which was constructively criticized by Professor Meester. This project was undertaken while I was receiving financial assistance from the CSIR and the traps were constructed using funds from the same source.

Table 1 Capture analysis according to species and mass in PVC (P) and hardboard (H) tunnel traps (NS = not significant; ** = highly significant; *** = very highly significant)

Species	Mass classes										Total captures		x^2	p	Significance
	Under 15,0 g		15,0 g - 29,9 g		30,0 g - 44,9 g		45,0 g - 59,9 g		60,0 g and over						
	P	H	P	H	P	H	P	H	P	H	P	H			
Otomys irroratus	-	-	-	1	-	-	1	2	17	64	18	67	28,25	,001>p	***
Rhabdomys pumilio	5	2	16	10	11	9	5	2	-	-	37	23	3,27	,10>p>,05	NS
Mus minutoides	8	-	-	-	-	-	-	-	-	-	8	0	8,0	,01>p>,001	**
Crocidura flavescens	-	-	4	4	7	2	-	-	-	-	11	6	1,47	,30>p>,20	NS
Myosorex varius	30	3	-	-	-	-	-	-	-	-	30	3	22,09	,001>p	***
Total captures	43	5	20	15	18	11	6	4	17	64	104	99	0,12	,80>p>,70	NS
x^2	30,08		0,71		1,69		0,40		27,27						
p	,001>p		,50>p>,30		,20>p>,10		,70>p>,50		,001>p						
Significance	***		NS		NS		NS		***						

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